

HOMING BEHAVIOR, NAVIGATION, AND ORIENTATION OF  
JUVENILE SEA TURTLES

by  
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## **ABSTRACT**

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Homing behavior, navigation, and orientation of juvenile sea turtles.  
(Under the direction of Kenneth J. Lohmann)

The present study was conducted to investigate homing behavior in juvenile sea turtles and to determine the mechanisms used by the turtles to navigate and orient. Homing behavior of juvenile loggerhead turtles captured in inshore waters was studied through a combination of mark-recapture techniques and radio telemetry. Turtles were tagged, displaced moderate distances, and released. Juvenile loggerheads were often recaptured both within a given year, as well as during subsequent years, and many displaced turtles returned rapidly to the capture area.

In addition, juvenile loggerhead and green turtles were displaced from capture sites and tested in an experimental arena to determine whether (1) the turtles exhibit homing behavior and migratory orientation in a controlled setting and (2) homing was accomplished using true navigation. Loggerhead and green turtles captured to the northeast of the testing site during the summer oriented in a direction that corresponded with the most direct path back to the capture area, as did loggerheads captured southwest of the testing site at the same time of year. Both loggerheads and green turtles tested during the fall oriented southward, which is a direction consistent with the migratory orientation observed in wild turtles at that time of year. These results indicate that the orientation behavior of loggerhead and green turtles in the arena setting accurately

reflects that of wild turtles and suggest that loggerheads are capable of map-based navigation.

Preferred orientation in the arena setting made it possible to begin investigation of the cues used by juvenile loggerheads to orient. Turtles established and maintained headings in specific directions in the absence of wave cues, familiar landmarks, and chemical gradients. Juvenile loggerheads were also able to maintain a consistent directional heading when either the magnetic field surrounding the anterior portion of the body was distorted using powerful magnets or when the turtles were outfitted with frosted goggles, which blocked visual cues. However, when the turtles experienced a simultaneous disruption of magnetic and visual cues their orientation was altered. These results demonstrate that juvenile loggerheads can use either magnetic or visual cues to orient, depending on which is available.

To my husband Chris, for his patience, understanding, assistance, and advice

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## CHAPTER 1

### INTRODUCTION

Although the definition of migration remains under debate, it is clear that many animals undertake diverse types of movements throughout their lives that vary in their nature and scale (reviewed by Dingle, 1996). Animals occupying distinct territories or home ranges undergo smaller-scale movements while foraging or seeking mates, as long as appropriate resources are present. Longer-distance movements often occur because the availability of suitable feeding and/or breeding areas is seasonal in nature. Such seasonality often necessitates movement between spatially separated areas to ensure that adequate resources can be obtained either at the appropriate time of year or year-round.

To be unequivocally designated as having carried out a true migration, the animal undertaking a long-distance journey must exhibit a variety of physiological and behavioral specializations (Dingle, 1996). Perhaps the best-known true migrations are those of birds, as many bird species conspicuously migrate hundreds or even thousands of kilometers between breeding and overwintering areas. The most extreme case is that of the Arctic tern (*Sterna paradisaea*), which travels an estimated 40,000-km round-trip between the Arctic and Antarctic each year, in the longest known migration (Alerstam, 1985). On a smaller scale, some large, terrestrial mammals such as caribou (*Rangifer tarandus*) migrate hundreds of kilometers between summer breeding areas and overwintering areas each year (Fancy et al., 1989).

In contrast, a number of birds and terrestrial animals do not exhibit specialized migratory adaptations and yet make long distance movements to gain access to seasonally abundant resources that are patchily distributed over a large area. Wandering albatrosses (*Diomedea exultans*) in the Southern Ocean make circuitous foraging flights 3664-15200-km in length (Åkesson & Alerstam, 1998). The movements of large ungulates such as wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) inhabiting the Serengeti plain in Africa occur in response to changes in the salinity of available drinking water and availability of preferred forage (Talbot & Talbot, 1963; Wilmshurst et al., 1999; Wolanski & Gereta, 2001). Likewise, some red deer populations (*Cervus elaphus*) undertake vertical, seasonal movements in montane habitat, following the appearance of edible vegetation as the snow line recedes (Albon & Langvatn, 1992). Female polar bears (*Ursus maritimus*) have also recently been shown to make circannual migrations, ranging widely in search of food, yet returning to specific locations at the same time each season, when resources become available at those sites (Mauritzen et al., 2001).

Similar to their terrestrial counterparts, marine animals exhibit true migrations, as well as non-specific, long-distance excursions, and in some cases their life histories may involve combinations of both types of movements. Satellite telemetry data obtained recently from whale sharks (*Rhincodon typus*) show three individuals traveling between 7762 – 12620 km in what were thought to be foraging movements along oceanographic features characterized by high productivity (Eckert & Stewart, 2001). Although little is known about shark migrations in general, these journeys may in fact be part of a circannual or multiannual migration to exploit seasonally localized aggregations of prey

(Wilson et al., 2001). Tuna range across oceanic basins in search of prey and are also thought to make directed migrations to reach appropriate spawning areas (Bremer et al., 1998; Nemerson et al., 2000; Rooker et al., 2001). Similarly, juvenile and adult seals travel hundreds of kilometers in search of food and then migrate long distances to specific rookeries when it is time to breed (Condit & LeBouef, 1984; Ronald and Dougan, 1982; McConnell et al., 2002). Various cetacean species also range widely within feeding areas. In addition, individuals of some species make annual true migrations spanning 6,000 - 20,000 km between their summertime polar feeding regions and specific wintertime breeding and calving areas in warm, protected, tropical waters. (Würsig, 1989; Gabriele et al., 1996; Watkins et al., 1996; Stevick et al., 1998; Sears & Larsen, 2002).

The life history of sea turtles appears to be similar to that of tuna, cetaceans, and pinnipeds, involving both true migrations and non-specific, long-distance excursions. Although sea turtles are predominantly aquatic, females remain bound to coastal beaches for reproductive purposes, laying their eggs in nests excavated in the sand (Miller, 1997). Hatchlings emerging from these nests immediately crawl to the ocean and migrate away from shore during a 'frenzy' period lasting approximately 24 h to reach the open ocean (Wyneken & Salmon, 1992).

Although juvenile flatback turtles (*Natator depressus*) are thought to remain in nearshore areas during their early years, the juveniles of other sea turtle species appear to lead a pelagic existence (reviewed by Musick & Limpus, 1997). For example, small

loggerheads (*Caretta caretta*) originating from beaches along the east coast of the US have been found in the east Atlantic (Bolten et al., 1998). Similar to their Atlantic counterparts, juvenile loggerheads originating from Japan have been found to feed off the coast of Baja, Mexico, after having crossed the Pacific Ocean (Bowen et al., 1995). In addition, juvenile loggerheads foraging along oceanic fronts in the North Pacific current system undergo seasonal, north-south movements that span thousands of kilometers (Polovina et al., in review).

After a period of maturation spent in the pelagic environment, larger juveniles undergo an ontogenetic habitat shift, recruiting to neritic areas and occupying demersal habitat (reviewed by Musick & Limpus, 1997). Along the coastal U.S.A., juvenile loggerhead, green (*Chelonia mydas*), and Kemp's ridley (*Lepidochelys kempii*) turtles inhabit inshore waters such as sounds, bays, and estuaries (Mendonça and Ehrhart, 1982; Mendonça, 1983; Lutcavage and Musick, 1985; Morreale et al., 1992; Epperly et al., 1995a). Juvenile green turtles occupy spatially restricted feeding areas (Mendonça, 1983) and graze repeatedly on specific grass beds (Bjorndal, 1980). Limited data and anecdotal reports suggest that juvenile loggerheads may also exhibit fidelity to preferred feeding areas (Byles, 1988). However, to date this issue has not been systematically addressed.

Because inshore water temperatures in some temperate and sub-tropical areas drop below lethal levels for sea turtles during the winter, juveniles inhabiting feeding grounds in those areas must migrate seasonally (Epperly et al., 1995a). Juvenile loggerhead,

green, and Kemp's ridley turtles migrate hundreds of kilometers south or southeast to reach warmer waters when temperatures drop and make the return journey north when waters again become habitable (Shoop & Kenney, 1992; Keinath, 1993; Epperly et al., 1995a,b).

As adults, turtles adopt resident feeding grounds, which they inhabit year after year (Limpus et al., 1992). Female sea turtles also exhibit fidelity to their natal beaches, returning to the areas where they were hatched to lay their own eggs (Meylan et al., 1990; Bowen and Karl, 1997). Thus, the turtles must periodically undergo long-distance migrations between spatially separated feeding and nesting areas (Meylan, 1995). Perhaps the most well-known and extreme case of this behavior involves the migration of green turtles from feeding areas along the coast of Brazil to nesting beaches on Ascension Island, over 2000 km away (Mortimer and Portier, 1989; Luschi et al., 1998). However, there are many other known examples of adult turtles migrating hundreds, or even thousands of kilometers to reach breeding/nesting areas (Limpus et al., 1992; Meylan, 1995).

The long-distance movements of sea turtles have elicited a great deal of interest because in many cases these animals cross vast expanses of seemingly featureless ocean to reach spatially restricted, specific destinations. These migratory feats have naturally caused researchers to question which sensory cues might be used to guide the turtles. In principle, turtles might use a number of different cues to orient and navigate. It has been proposed that sea turtles might be able to use bathymetry and/or landmark cues in

familiar areas to guide themselves toward their goal (Luschi et al., 1996; Luschi et al., 1998). However, in many cases migrations occur in water deep enough that the turtles would have to use alternative cues.

It has also been hypothesized that sea turtles might orient toward their destination based on sensory contact with the goal. Salmon imprint to the chemical characteristics of their natal streams and are able return to appropriate spawning areas through later recognition of these stream-specific odors (Hasler and Scholz., 1983). Koch et al. (1969) postulated that female green turtles migrating from Brazil to their nesting beaches on Ascension Island might also use this method of orientation by following a chemical gradient carried by the South Equatorial Current to reach their destination. As sea turtles are capable of detecting chemicals underwater at low concentrations (Manton et al., 1972), it is possible that they might recognize and respond to odors during homing under natural conditions. However, the migratory paths of sea turtles often do not coincide with prevailing currents (Papi et al., 1995); therefore it is likely that other guidance cues are used.

Other cues apart from landmarks and chemical gradients can also be used to set and maintain headings (Able, 2000; Papi, 1992). Under some conditions, ocean waves can provide directional information for aquatic animals (Lohmann et al., 1990; Lohmann et al., 1995). Furthermore, many animals orient by using compass senses based on celestial information. Sandhoppers obtain information about the land-sea axis from the position and phase of the moon, despite the irregularity of its cycle (Papi and Pardi, 1963) and



many birds that undergo nocturnal migrations use a star compass (Wiltschko et al., 1998). Diurnally active animals can obtain compass information from the most prominent feature of the daytime sky, the sun. The role of the time-compensated sun compass in the homing behavior of pigeons has been well-documented (reviewed by Schmidt-Koenig et al., 1991) and its use has also been noted in freshwater and terrestrial turtles (DeRosa and Taylor, 1980), as well as in fish (Hasler et al., 1958; Winn et al., 1964; Levin et al., 1992). In addition, directional information can be obtained from the pattern of sunlight polarization. This information is used by ants during path integration (Wehner et al., 1996), by birds during migratory movements (Able, 1989), and also by several fish species (Waterman and Forward, 1970; Hawryshyn et al., 1990). Organisms from diverse taxa have also been found to use compasses based on either the polarity of the earth's magnetic field or its inclination angle, which is the angle at which the field lines intersect the surface of the earth (reviewed by Wiltschko and Wiltschko, 1995).

However, aquatic animals are often subject to displacements caused by waves and currents that would interfere with maintaining a constant heading (Mayne, 1974). It has therefore been hypothesized that the ability to determine geographical position using only local cues, or true navigation (Griffin, 1952; Phillips, 1996), is necessary for sea turtles to reach their desired destinations (Papi et al., 1995; Lohmann et al., 1997; Lohmann and Lohmann, 1998; Luschi et al., 1998). True navigation might be accomplished by using (1) components of a mosaic map, such as landmarks or chemical cues, or (2) magnetic features.

In the case of a mosaic map, animals build up a mental map of characters within their familiar area and learn the relationship of those characters relative to one another, as well as to home, as compass directions (Wallraff, 1991; Papi, 1992; Able, 2000). Pigeons are thought to use a mosaic map of landmarks to orient in the familiar area surrounding their loft (W. Wiltschko and Wiltschko, 1978; Wallraff et al., 1994). In addition, another unusual form of mosaic map has been proposed for these birds, whereby pigeons at the loft obtain directional information from odors carried on the wind (Papi, 1991; Papi and Wallraff, 1992). If displaced to an unfamiliar location, the pigeons would theoretically associate the odor of that location with the direction from which the wind carried that particular odor and then orient appropriately toward home. So, for example, if a pigeon at its loft were to consistently associate odor X with a southerly wind, if the pigeon found itself in an area that smelled of odor X, it would know that it needed to fly north to reach the loft. However, given the dynamic nature of atmospheric conditions, it is currently unclear whether odorants might remain stable enough over time for pigeons to learn their relationship relative to the loft (Wallraff, 1991). Also, it is unlikely that this sort of olfactory map could account for the ability of pigeons to home over distances of hundreds or even thousands of kilometers (Wallraff, 1991).

At any geographic location, the earth's magnetic field can be characterized by a number of features (reviewed by Wiltschko and Wiltschko, 1995). Among those are the field's intensity, or strength, and its inclination angle. These characteristics vary somewhat regularly over the surface of the earth; inclination angle and intensity values are high near the poles and low near the equator. Experiments involving a number of

different animals, including sea turtles, have provided evidence that supports the use of such magnetic information to determine approximate geographic position (Rodda, 1984; Fischer et al., 2001; Franson et al., 2001; Lohmann et al., 2001; Phillips et al., 2002; Boles and Lohmann, 2003).

The orientation cues used by hatchling sea turtles during their migration away from the beach have been extensively investigated. Hatchling loggerheads are able to use both wave surge (Wang et al., 1998) and the orbital motion of waves (Lohmann et al., 1995; Manning et al., 1997) to set and maintain an offshore course. In addition, loggerhead and leatherback (*Dermochelys coriacea*) hatchlings are able to use a magnetic compass to orient, which presumably serves to keep the turtles on an offshore course when waves are no longer a reliable indicator of the offshore direction (Lohmann, 1991; Lohmann and Lohmann, 1993). The magnetic compass used by loggerhead hatchlings is similar to that of birds (Light et al., 1993), involving the perception of the angle between the gravity vector and the angle at which the magnetic field intersects the earth (Wiltschko and Wiltschko, 1972).

Furthermore, hatchling loggerheads are able to detect two separate components of the Earth's magnetic field, inclination angle and total intensity (Lohmann and Lohmann, 1994,1996). Hatchling loggerheads exposed to combinations of inclination and intensity that are found in different locations around the North Atlantic Gyre exhibit directional orientation appropriate to keep them within the confines of the gyre; thus, these

components appear to provide the hatchlings with at least an approximation of their geographic position (Lohmann et al., 2001).

Despite the wealth of knowledge about hatchling orientation, the cues used by older turtles, as well as most other marine migrants, remain unknown. This is in part because studying orientation behavior in large, underwater animals that are powerful swimmers and range over large distances has proven difficult. However, it is possible that the navigational mechanisms used by juvenile and adult turtles differ from those used by hatchlings. For other animals such as pigeons and migratory birds, the relative importance of orientation cues changes as the animals mature (Wiltschko, 1983; Wiltschko and Wiltschko, 1998). Furthermore, sea turtles undergo multiple ontogenetic habitat shifts throughout their lives (Musick and Limpus, 1997) and the utility of different cues might vary between habitats.

The purpose of the present study was to investigate the homing behavior and migratory orientation of juvenile sea turtles inhabiting inshore waters and then to use this behavior to determine which cues the turtles might use to navigate and orient. The specific objectives of this study were: 1) to determine whether juvenile loggerhead sea turtles inhabiting the inshore waters of North Carolina would exhibit site fidelity and homing behavior in the wild, 2) to ascertain whether juvenile loggerhead and green sea turtles exhibit homing and migratory orientation in a controlled setting and whether homing is accomplished using true navigation, and 3) to investigate the sensory cues used by juvenile loggerheads to orient.

To investigate site fidelity and homing behavior in juvenile loggerheads occupying inshore waters, a mark-recapture study spanning four years was conducted in Core Sound, North Carolina. Each year of the study, approximately half of the turtles captured were tagged and released near the capture site, while the other half was displaced 15-20 km and released. Radio telemetry was also used to follow the movements of a small number of displaced turtles more closely.

Experiments were also conducted to determine if juvenile sea turtles exhibit homing and migratory orientation in a controlled setting, as well as to ascertain whether homing was accomplished using true navigation. Juvenile loggerheads were displaced from capture locations to the northeast and southwest of a testing site during the summer and allowed to swim in an experimental arena to determine whether turtles from both sites exhibited orientation consistent with the most direct path back to their respective capture areas. In addition, both loggerhead and green turtles captured to the northeast were tested to determine whether they exhibit homeward orientation during the summer and southward orientation during the fall, which corresponds to the migratory orientation observed in wild turtles at that time of year.

Finally, experiments were conducted to investigate the orientation cues used by juvenile loggerheads. Turtles were tested to determine whether they were able to set and maintain consistent directional headings in the absence of wave cues, familiar landmarks, and chemical gradients. Juvenile loggerheads were also tested under conditions in which

magnetic and/or visual cues were disrupted to determine which cues were necessary to maintain a heading.

The study of homing behavior in juvenile loggerhead turtles has implications for the conservation of the species. Dredges are regularly used to deepen shipping channels and the use of hopper dredges has been implicated in the mortality of large numbers of turtles (National Research Council, 1990). In an attempt to minimize turtle mortality, efforts have been made to remove turtles from a given channel and to release them some distance away from the proposed dredging site (Dickerson et al., 1995). However, if loggerheads exhibit site fidelity and quickly return to the location in which they were originally captured, then this strategy will not be effective in mitigating turtle mortality during dredging.

Investigation of homing behavior and seasonal migratory orientation in a controlled setting, such as the experimental arena used in this study, provides a novel means of studying the orientation and navigation of juvenile sea turtles. The results have provided insight into the sensory cues used by both juvenile turtles during short-distance movements, such as homing, as well as during longer migrations. At the same time, this study may give insight into the navigational information used by adult turtles, as well as other marine migrants.

## **CHAPTER 2**

### **SITE FIDELITY AND HOMING BEHAVIOR IN JUVENILE LOGGERHEAD SEA TURTLES**

#### **Introduction**

Almost immediately after emerging from their nests, hatchling loggerheads originating from the east coast of the U.S.A. migrate offshore from their natal beaches to reach the open ocean (Salmon & Wyneken, 1987). The turtles spend the first years of their lives in the North Atlantic Gyre, a circular current system that encompasses the Sargasso Sea (Bolten et al., 1998; Carr, 1986, 1987).

After residing in the pelagic environment for a period of years, juvenile loggerheads return to the east coast of the U.S.A. and inhabit inshore waters such as sounds, bays, and estuaries in sub-tropical to temperate regions (reviewed by Musick and Limpus, 1997). Sea turtles occupying foraging areas where water temperatures fall below lethal levels during the winter must migrate seasonally, moving to warmer, southern waters in the fall and returning to northern foraging grounds in the spring (Epperly et al., 1995a,b; Keinath, 1993; Morreale & Standora, 1995; NMFS, Beaufort Laboratory, unpub. data; Shoop and Kenney, 1992). Little is known about the patterns of residence, habitat utilization, or movements of juvenile loggerheads occupying foraging areas in inshore waters. Limited data and anecdotal reports suggest that juvenile loggerheads exhibit site fidelity within preferred areas and that they sometimes return to specific sites after having completed

seasonal migrations or after being displaced (Byles, 1988; Dickerson et al., 1995; Lutcavage and Musick, 1985; Mendonca & Ehrhart, 1982). These issues have not, however, been systematically studied.

To investigate site fidelity in juvenile loggerheads, mark-recapture data spanning a four-year period were examined to determine if turtles caught at specific locations were recaptured at those same sites during the year of their initial capture, as well as during subsequent years. In addition, recapture data for turtles released at the capture site and those released at sites 15-20 km distant were analyzed to ascertain whether the turtles exhibited homing behavior. Several displaced turtles were also followed using radio telemetry to monitor homing more closely. The results of this study provide evidence that the turtles display site fidelity both within a single foraging season, as well as between years. Moreover, they imply that juvenile loggerheads possess the navigational abilities needed to return to specific locations after long-distance migrations and forced displacements.

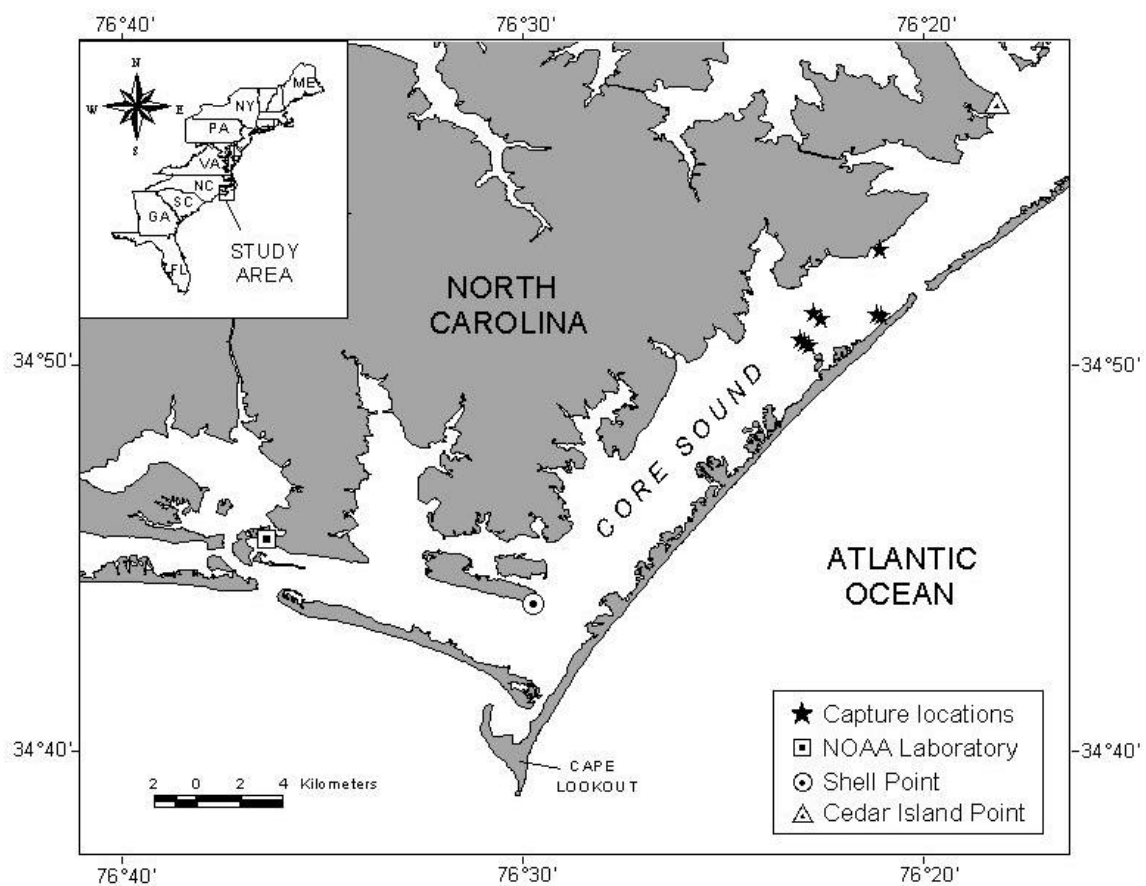
## **Materials and methods**

### *Study area*

The study was conducted in Core Sound, North Carolina, U.S.A. (Fig. 2.1). Core Sound is relatively shallow (2-3 m deep), and is separated from the Atlantic Ocean by a series of barrier islands (Ferguson et al. 1993). Juvenile loggerhead turtles reside in the sound during the spring, summer, and early fall, leaving inshore waters when water temperatures begin to decrease in mid- to late fall and returning again in the spring



Figure 2. 1. Map of Core Sound, located in North Carolina on the eastern coast of the United States. Turtles were captured at the locations indicated by the stars on the map and were then either released near the capture site or displaced. The NOAA laboratory, where displaced turtles were held, is shown as a square on the map. Displaced turtles were released either at Shell Point (location indicated by circle), approximately 20 km southeast of the capture sites or Cedar Island Point (location indicated by triangle), which is located about 15 km northeast of the capture area.



(Epperly et al. 1995a,b). The study was therefore carried out between May and December of each year from 1998 to 2001.

### *Turtle capture and tagging*

Juvenile loggerheads were captured using pound nets, a type of passive, stationary, fishing gear that retains turtles but allows them to surface to breathe (see Fig. 2.1 for capture locations). Pound nets in the study location were fished twice a week from mid-May until the first week in December (as weather allowed) during each year of the study and the geographic coordinates of capture locations were determined using a hand-held Global Positioning System (GPS) unit.

Turtles were marked with two Inconel Style 681 flipper tags (National Band and Tag, Newport, Kentucky, USA), one on the trailing margin of each rear flipper. In addition, a 125 kHz unencrypted Passive Integrated Transponder (PIT) tag (Destron-Fearing Corp., South St. Paul, Minnesota, U.S.A.) was injected subcutaneously above the second most proximal scale of the trailing margin of the left front flipper. Standard straight-line carapace lengths (SCL) were taken to the nearest 0.1 cm.

### *Mark-recapture*

Each year from 1998 to 2001, approximately half of the loggerheads captured were tagged and released near their capture sites. The remainder of the turtles caught each year were displaced either approximately 20 km southwest of the capture site to Shell Point (Fig. 2.1) or approximately 15 km northeast to Cedar Island Point (Fig. 2.1) and

released. Displaced turtles were first transported to shore along a convoluted route and then driven in a covered vehicle along winding, coastal roads to the National Oceanic and Atmospheric Administration (NOAA) laboratory in Beaufort, North Carolina, located approximately 30 km southwest of the capture area (Fig. 2.1). For logistical reasons, displaced turtles were held at the NOAA laboratory between 48 and 72 h before again being transported in a covered vehicle along winding roads to either Shell Point or Cedar Island Point. Although turtles might occasionally have been able to glimpse the sky while on the fishing vessel, they were generally not able to view their surroundings and the sky during transport.

Only those turtles caught and displaced between May and September were considered for the homing study because turtles begin to migrate out of inshore waters in October or November (Epperly et al. 1995a). The tag numbers and capture locations of any recaptured turtles were recorded for later analysis.

### *Radio telemetry*

To monitor their movements after release, 28 of the loggerheads displaced to Shell Point and Cedar Island Point during 1998, 1999, and 2000 were outfitted with MOD-050 radio transmitters (164-165 MHz) with TA-6L antennas (Telonics, AZ). Four of these loggerheads were tracked in two separate years. To attach the transmitters, a 0.5 cm diameter hole was first drilled through one of the turtle's pygal bones at the rear margin of the carapace, as well as the overlying scutes, with a drill bit scrubbed with Betadine disinfectant. A plastic electrician's tie was then passed through the hole and secured.

Transmitters were housed in bullet-shaped buoys (approximately 10 cm diameter and 10 cm in height) secured to one end of a 0.5 m tether that consisted of 1 mm diameter stainless steel fishing leader. The tether was then connected to the plastic tie in the turtle's shell with a ball-bearing swivel and two short lengths of either 30 lb. spiderwire or 30 lb. test monofilament fishing line. This configuration allowed the turtles to break free if either the buoy or tether became entangled in submerged or floating debris, or bottom structure.

Tracking was accomplished using a Telonics TR-2 Receiver (164/166 MHz) with a TS-1 Scanner/Programmer, in combination with a 4-element, hand-held, Yagi antenna (AVM Instrument Company, Ltd., CA). Beginning 12 to 24 h after release, each turtle was tracked daily from the western shoreline of Core Sound. When a transmitter signal was detected, the bearings at which the signal could no longer be heard were determined and the direction of the transmitter was taken as the line that bisected those bearings (Kenward 2001). A compass bearing was then taken along that line using a hand-held, digital compass (Autohelm, Portsmouth, England). Because radio waves do not transmit well through salt water and transmitters were generally submerged when turtles were not at the surface, transmitter signals were only detected when turtles surfaced to breathe. Therefore, a constant signal signified that the transmitter had become detached.

During tracking, I sequentially obtained between two and four bearings for each animal's position and then plotted those bearings on a nautical chart. On a given day, a turtle's location was taken to be either the point where all bearings intersected or the

center of the polygon formed when three or four bearings did not precisely intersect one another (Byles 1988). True positional error is not reported here because bearings were not obtained simultaneously and therefore the turtles' movements between the times at which bearings were taken would have made it impossible to determine their locations precisely. However, the sizes of the polygons formed when 3-4 bearings were plotted to determine a turtle's position were generally less than 1 km<sup>2</sup>; thus, the locations obtained with this method were sufficiently precise to determine whether or not the turtles had returned to the vicinity of their capture area.

For those turtles that retained their transmitters longer than 1 d but were not successfully followed long enough to obtain homing data, the location at which a turtle was last detected still bearing its radio transmitter was used to obtain information regarding direction of movement. The final positional fix obtained for a turtle was plotted on a nautical chart and the compass bearing between the release site and that location was then measured. These headings were then analyzed with standard procedures for circular statistics (Batschelet, 1981) to determine whether the turtles were significantly oriented in a direction that corresponded with the most direct path back to the capture location.

#### *Data analysis*

Recapture data were analyzed (1) to test for differences between the proportion of turtles recaptured after being displaced versus the proportion recaptured after being released near their capture locations and (2) to determine whether there was a difference

between the proportion of turtles recaptured after being displaced 20 km south to Shell Point and the proportion recaptured after being displaced 15 km north to Cedar Island Point. Chi-square tests were used to make these comparisons except when recapture numbers were too small; in these cases, the Fisher Exact test was used instead (Zar 1996). Although turtles were occasionally displaced more than once, only a turtle's first displacement was included in the analysis of homing data to avoid problems with statistical independence. The Kolmogorov-Smirnov Two-Sample test (Sokal and Rohlf 1981) was used to determine whether there was a difference between the sizes of those turtles that were recaptured and those that were not recaptured.

## **Results**

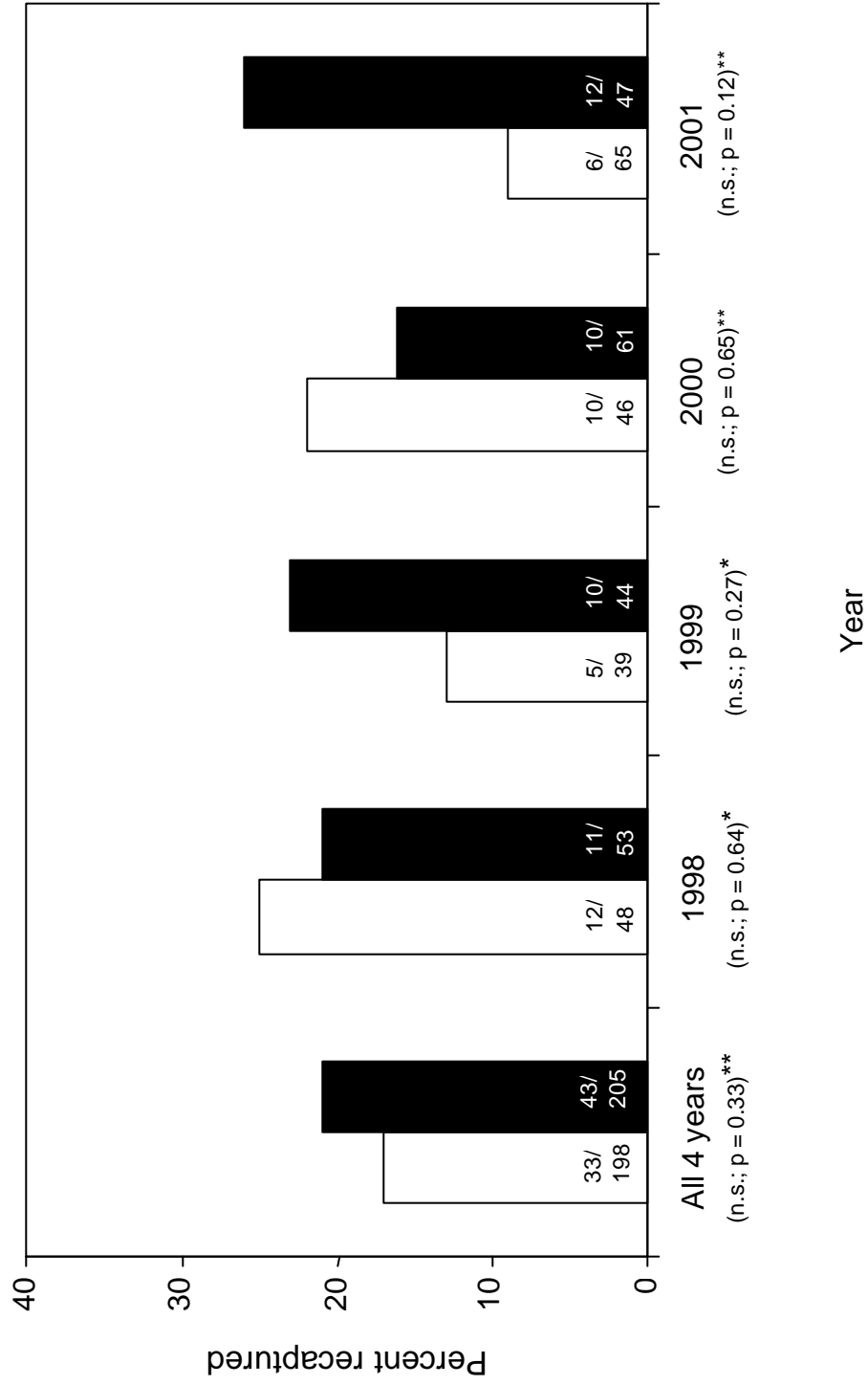
Between 1998 and 2001, 405 loggerheads ranging from 42.3-86.8 cm SCL (Mean = 61.7 cm; SE = 0.38 cm) were captured. Of these, 207 turtles were tagged and released near their capture sites (Figs. 2.1 and 2.2). Throughout the study, 21% of these turtles were recaptured during the same year that they were tagged (see Fig. 2.2 for data from individual years). In addition, 198 loggerheads were displaced to locations either 20 km south or 15 km north and released (Figs. 2.1 and 2.2). Over the course of the study, 17% of all displaced turtles were recaptured in the same year they were released (see Fig. 2.2 for data for individual years). The proportions of turtles recaptured after being released near the capture location and after being displaced were not significantly different ( $\chi^2$  Test and Fisher Exact Test,  $p > 0.05$  in all comparisons; Fig. 2.2).

Fig. 2.2. Recapture percentages of displaced and non-displaced juvenile loggerheads.

White bars represent displaced turtles and black bars represent non-displaced turtles. The proportions of displaced and non-displaced turtles recaptured within a given year, as well as over all four years of the study were not significantly different from one another ( $p>0.05$  in all cases; \* denotes use of two-tailed Fisher Exact Test and \*\* denotes use of Chi-square analysis with Yates correction).



Recapture percentages of displaced vs. non-displaced loggerheads



From 1998 to 2001, 36% of the non-displaced turtles that were recaptured were caught in the same net as in their original capture and 30% were recaptured more than once; 10 turtles were recaptured twice and three turtles recaptured three times each. Similarly, 32% of the turtles recaptured after being displaced were caught in the same net as in their original capture and 29% were recaptured more than once. Five turtles were recaptured twice, three were recaptured three times, and two were recaptured five times over periods of several months.

Throughout the study, 20% of turtles displaced to the southwest and 10% of the turtles displaced to the northeast were recaptured during the year they were displaced (see Fig. 2.2 for data from individual years). The proportions of turtles recaptured after being displaced southwest vs. northeast were not significantly different (Chi-square analysis and Fisher Exact test,  $p > 0.05$  in all comparisons; Fig. 2.2). Intervals between release of displaced turtles and their recapture ranged from 1 to 95 d (Mean = 26 d; SD = 24 d). Of the turtles recaptured after displacement, 26% were caught less than one week after being released and 45% were caught in less than two weeks.

In addition to those turtles recaptured during the year in which they were first tagged, a number of both displaced and non-displaced turtles were recaptured at least once in following years (Tables 2.1 and 2.2). Many turtles were caught multiple times during those subsequent years (Table 2. 3), 53% of those in the same net in which they were originally captured. There was no significant difference between the sizes of the

Figure 2.3. Recapture percentages of juvenile loggerheads displaced 20 km southwest or 15 km northeast of their capture area. Black bars represent turtles displaced southwest and white bars represent turtles displaced northeast. The proportions of turtles recaptured from the two sites within a given year, as well as over all four years of the study, were not significantly different from one another ( $p > 0.05$  in all cases; \* denotes use of two-tailed Fisher Exact Test and \*\* denotes use of Chi-square analysis with Yates correction).

Recapture percentages of loggerheads displaced southwest vs. northeast

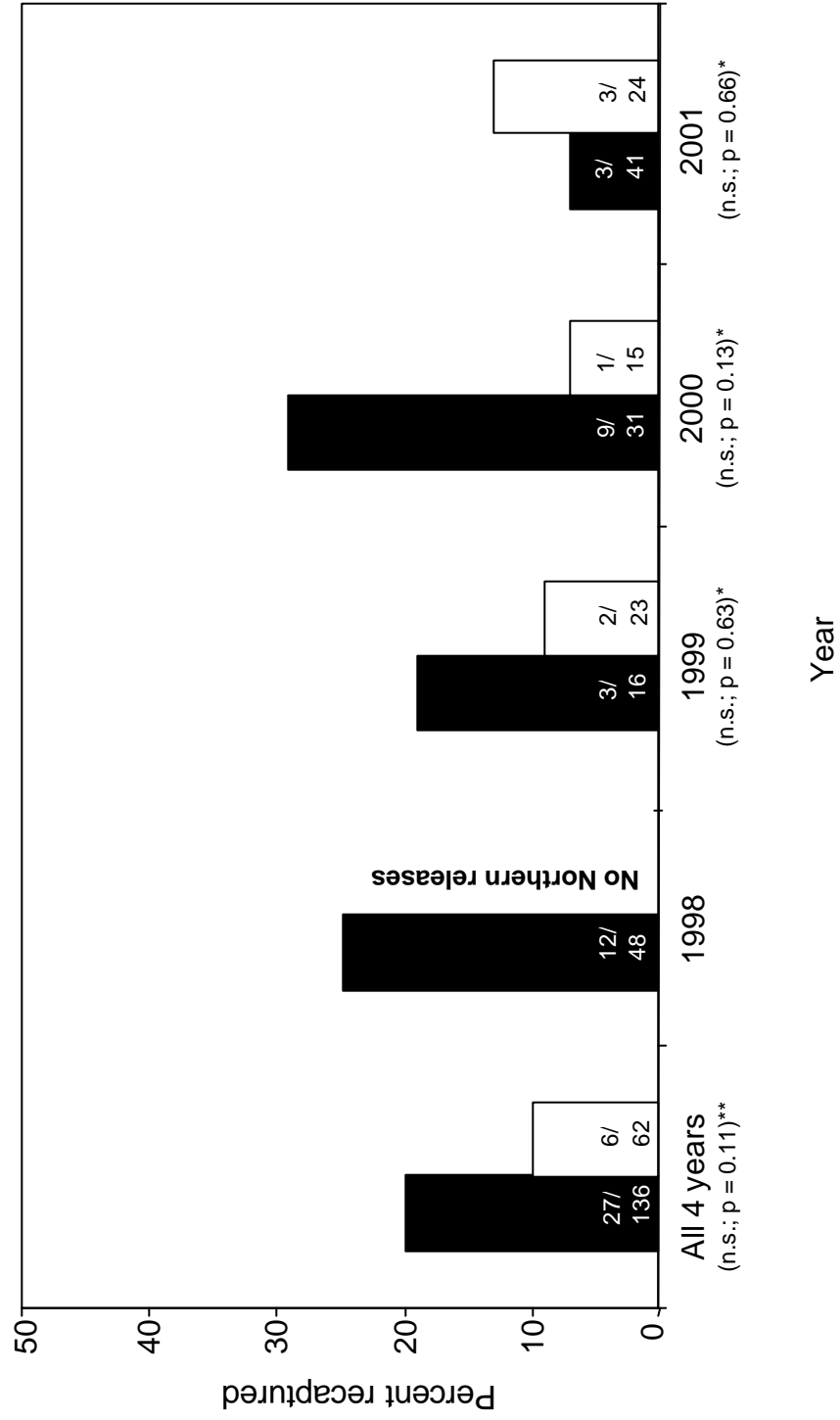


Table 2.1. Summary of displaced loggerheads recaptured throughout the study					
Year of displacement	Number displaced	Number recaptured in 1998	Number recaptured in 1999	Number recaptured in 2000	Number recaptured in 2001
1998	48	12 (25%)	6 (13%)	7 (15%)	7 (15%)
1999	39	-	5 (13%)	8 (21%)	2 (7%)
2000	46	-	-	10 (22%)	3 (7%)
2001	65	-	-	-	6 (9%)

Table 2.2. Summary of non-displaced loggerheads recaptured throughout the study					
Year of capture	Number not displaced	Number recaptured in 1998	Number recaptured in 1999	Number recaptured in 2000	Number recaptured in 2001
1998	53	11 (21%)	2 (4%)	6 (11%)	4 (7%)
1999	44	-	10 (23%)	5 (11%)	3 (7%)
2000	61	-	-	10 (16%)	7 (11%)
2001	47	-	-	-	12 (26%)

Table 2.3. Summary of all loggerheads tagged 1998-2000 and recaptured in subsequent years

Master tag number	Number of times captured in 1998	Number of times captured in 1999	Number of times captured in 2000	Number of times captured in 2001
PPZ555	6	4	2	2
PPZ562	2	0	0	1
PPZ908	1	0	2	0
QQT580	1	0	1	0
QQT596	1	0	2	0
QQT934	2	0	2	1
QQT949	1	1	0	0
QQT984	2	3	0	1
QQT994	1	0	3	2
QQV237	4	0	1	0
SSR153	1	0	1	0
SSR173	1	0	1	0
SSR184	1	0	0	1
SSR192	3	1	0	1
SSR294	1	0	1	0
SSR327	2	3	2	1
SSR427	2	3	1	1
SSR453	1	1	0	2
SSW601	-	1	1	0
SSW641	-	1	1	0
SSW689	-	1	1	0
SSW695	-	1	4	3
SSW702	-	1	1	0
SSW720	-	1	1	0
SSW725	-	2	1	0
SSW759	-	1	2	1
SSW766	-	1	1	0
XXE012	-	-	1	1
XXE041	-	-	1	1
XXE081	-	-	2	1
XXE097	-	-	1	1
XXE102	-	3	6	2
XXE110	-	1	1	0
XXE202	-	-	1	3
XXE247	-	-	1	4
XXE288	-	-	2	2
XXE300	-	-	1	4
XXE430	-	-	1	1

(- turtle not yet captured for the first time)

turtles recaptured and those not recaptured throughout the course of the study ( $p=0.20$ , Kolmogorov-Smirnov Two-Sample Test).

Homing data were obtained from four telemetered turtles, one of which was tracked during two separate years. Of the four turtles that were successfully tracked using radio telemetry, all four returned to the vicinity of their capture locations within 3-5 days of release (Figs. 2.4 – 2.7). While one turtle (Cc73) was recaptured multiple times following its release at Shell Point, the other three telemetered turtles were not subsequently recaptured despite having returned to the capture area.

For those turtles that retained their transmitters 1 d or more but were not continuously tracked because of logistical difficulties, the final positional fixes obtained for each turtle were used to plot directional headings. Thirteen headings were obtained for turtles released at Shell Point and these individuals were significantly oriented in their homeward direction (Fig. 2.8). Only two of the turtles released at Cedar Island Point retained their transmitters for one day or longer. The initial headings of these individuals were  $152^\circ$  and  $185^\circ$ , yielding a mean angle of  $169^\circ$  (Homeward direction =  $224^\circ$ ). However, the sample size was too small to perform statistical analysis.

Apart from the five successful tracks, during the remaining 27 telemetry attempts 16 turtles lost their transmitters in 1 d or less, 7 turtles lost their transmitters after 2-3 d, and



Figure 2.4. Radio track of loggerhead *Cc73*. This turtle was caught for the first time 23 July 1999 and was recaptured 17 July 2000. After being outfitted with a transmitter and released at Shell Point, *Cc73* returned to the capture area in 4 d, swam back southwest, and then lost its transmitter. The turtle was recaptured again three times in the same location several hundred meters east of the 1999 and original 2000 capture site. These recapture events made it possible to re-outfit *Cc73* with a transmitter twice and release the turtle near the capture site. The brief tracks subsequently obtained before the turtle again entered a pound net and lost its transmitter combined with the turtle's recaptures showed that *Cc73* remained close to the capture location, which suggests that the turtle likely stayed in the area for a period of several months. *Inset*: Close-up view of 1999 and 2000 capture locations, along with two additional short tracks obtained after the turtle was recaptured and subsequently released after being re-outfitted with a radio transmitter.

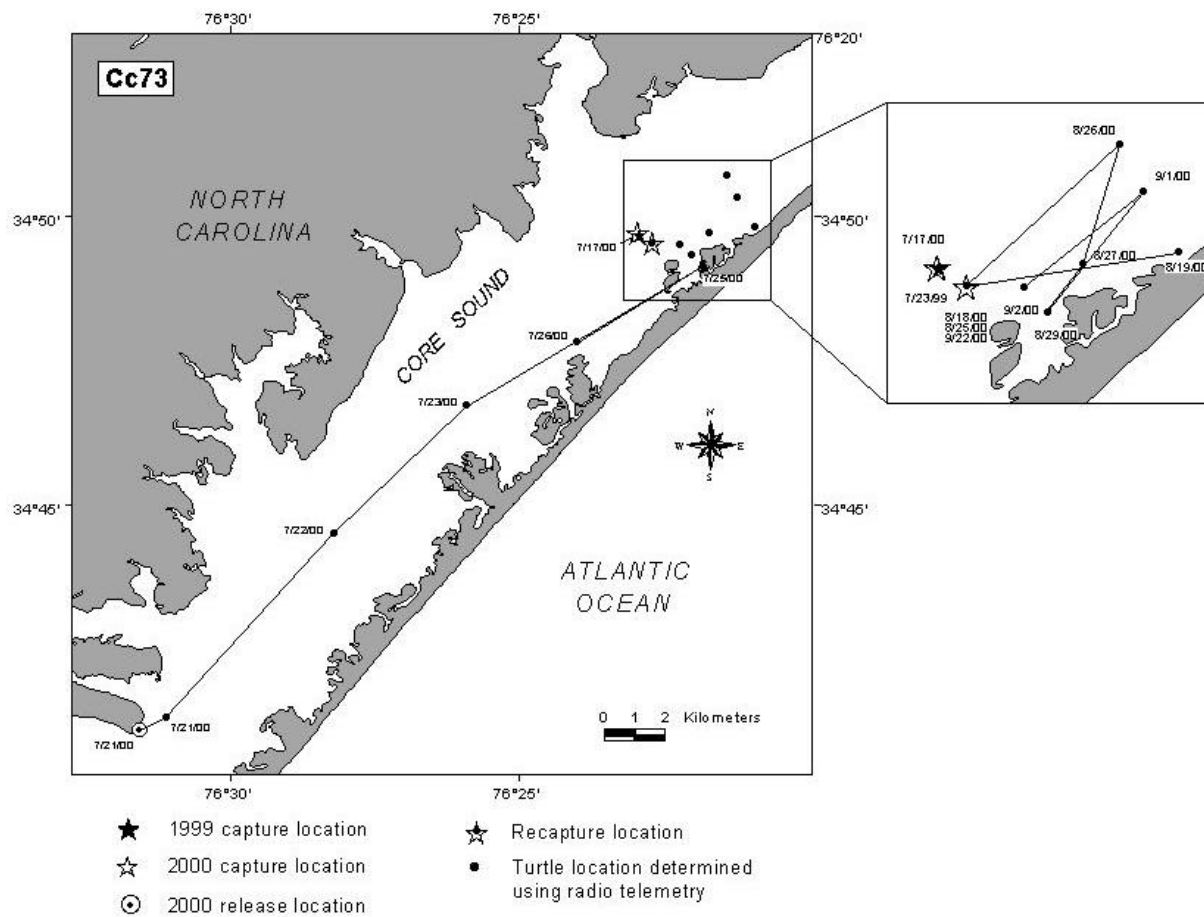


Figure 2.5. Radio track of loggerhead *Cc24*. This turtle was initially captured in 20 July 1998, outfitted with a transmitter, and released 20-km southwest of the capture site at Shell Point on 23 July 1998. It was tracked to the capture location within 5 d of being released, at which point the turtle lost the transmitter. *Cc24* was recaptured 4 August 2000 at the same location as in 1998 and was again displaced to Shell Point, outfitted with a transmitter, and released 7 August 2000. The turtle returned to the capture site in three days, but continued moving until it reached a location 5-km northeast of the capture site and remained there for approximately 7 d before it lost its transmitter.

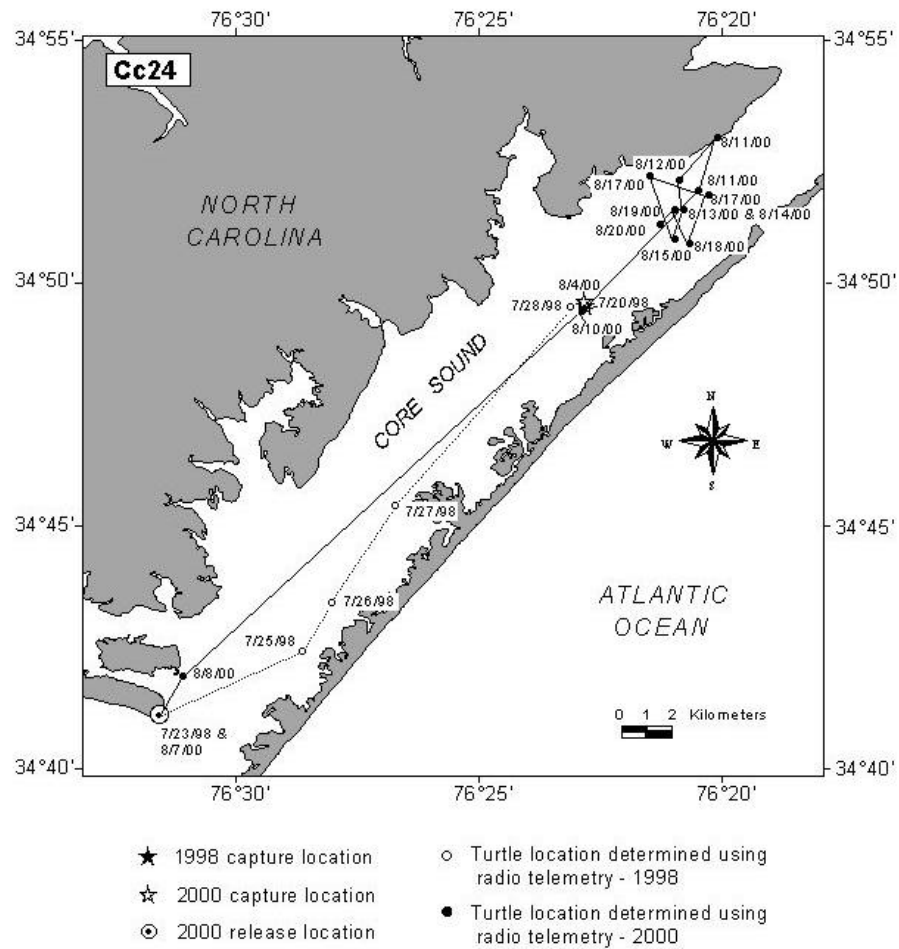


Figure 2.6. Radio track of loggerhead *Cc89*. This turtle was caught 23 August 1999 and again on 18 August 2000 at a location 6.5-km northeast of the 1999 capture site. After being displaced to Shell Point and released with a transmitter 19 August 2000, the turtle returned to the vicinity of the 1999 capture location in 3 d and continued to move north until it reached a location slightly northeast of the 2000 capture site. The turtle remained there for 6 d and then lost its transmitter.

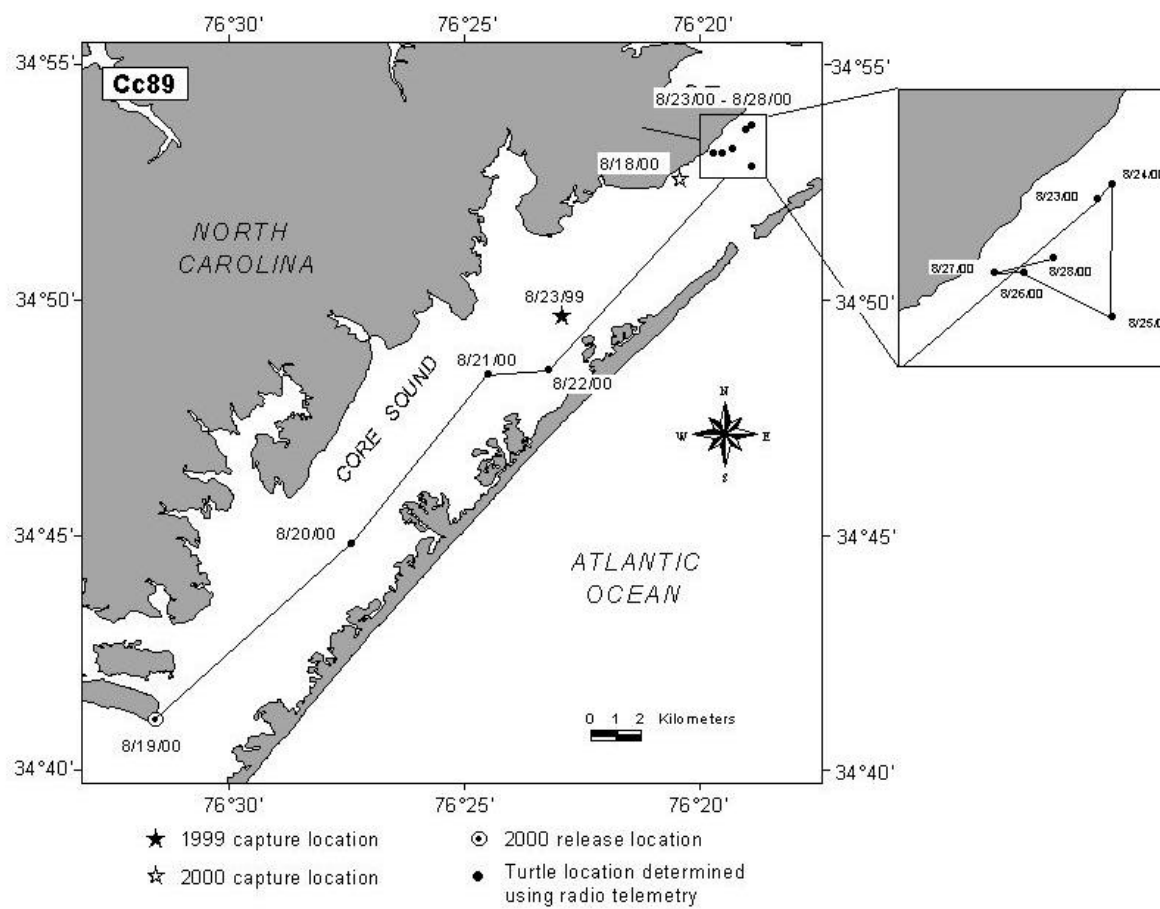


Figure 2.7. Radio track of loggerhead *Cc29*. This turtle was captured 6 August 1998, displaced to Shell Point, and released 9 August, 1998. The turtle reached a location approximately 5-km northeast of the capture location 5 d after being released. *Cc29* then continued to move until it reached a location about 10-km northeast of the turtle's capture site and remained in this area until it lost its transmitter 7 d later.

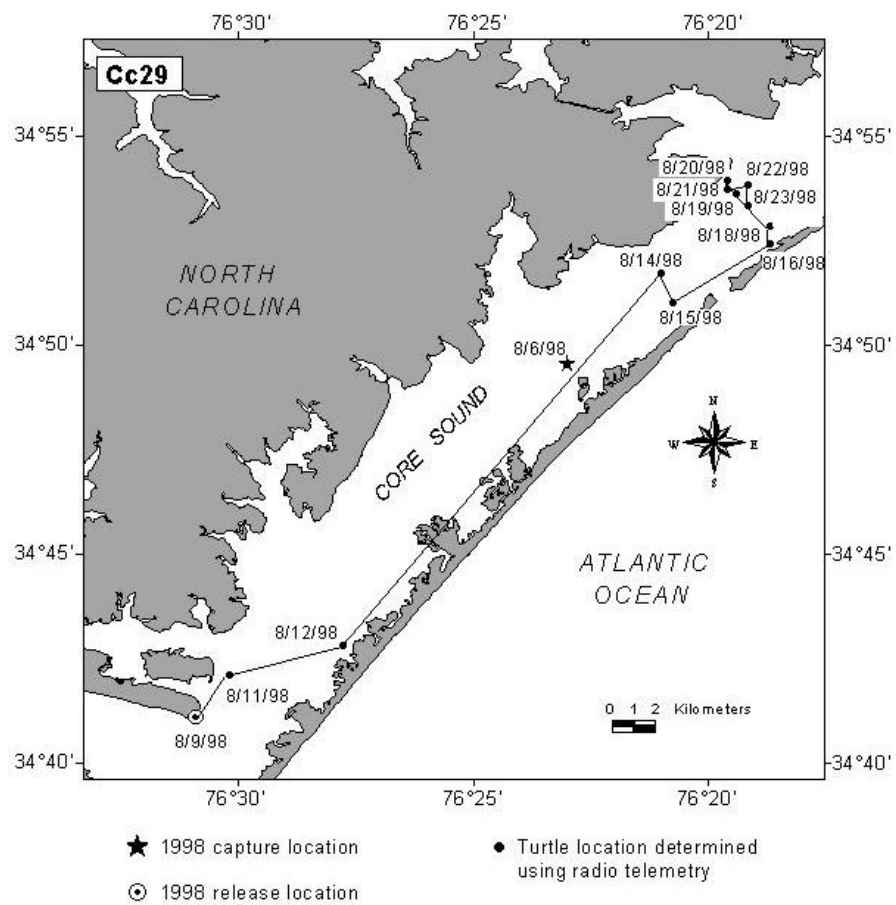
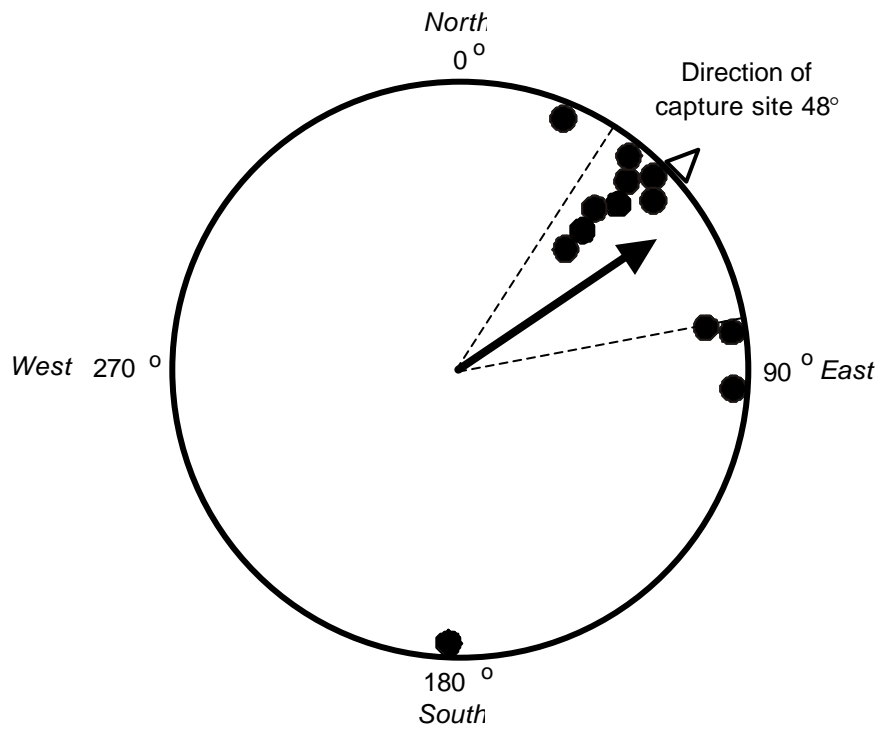




Figure 2.8. Initial directional headings of juvenile loggerheads released from Shell Point, 20-km southwest of their capture location (headings of turtles successfully tracked not included in this analysis). The location at which a turtle was last detected still bearing its radio transmitter was plotted on a nautical chart and the angle between the release site and that location was then determined as the turtle's vanishing bearing. Each dot within the circular diagram corresponds to the vanishing bearing for an individual turtle and the triangle on the outside of the circle corresponds to the direction of the capture area (48°). The dotted lines represent the boundaries of the 95% confidence interval. The distribution was significantly oriented with a mean angle of 56° (n=13,  $r=0.82$ ,  $p<0.001$  Rayleigh test, 95% confidence interval  $\pm 23^\circ$ ), a direction that corresponded very closely with the most direct path back to the capture area.

# Shell Point releases



15 turtles lost their transmitters after 4-7 d of intermittently successful tracking efforts. Recovery of lost transmitters showed that attachment failed both when the breakaway links were severed, as well as when the electrician's tie secured through a hole in the carapace snapped. This suggests that the transmitter attachment method used in this study may not be optimal in shallow, inshore waters that may contain a large amount of benthic structure, fishing gear, and debris which could entangle the transmitters and/or their tethers.

## **Discussion**

Over the course of the study, the proportions of displaced and non-displaced turtles recaptured in the vicinity of their original capture sites were not significantly different. These data imply that displaced turtles frequently homed to the locations where they were captured, because if turtles dispersed randomly or remained where they were released, then fewer displaced turtles than non-displaced turtles should have been recaptured. Thus, the results indicate that juvenile loggerheads exhibit site fidelity and that individuals displaced from their capture locations possess the ability to navigate back to particular sites.

In addition to the recaptures observed within a given year, a number of turtles were recaptured in the vicinity of their original capture sites in following years. Inshore water temperatures in the sounds of North Carolina drop below lethal levels ( $<10^{\circ}\text{C}$ ; Schwartz, 1978) for sea turtles during the winter months (Epperly et al. 1995c). Juvenile loggerheads migrate offshore and/or south to warmer waters during the winter and

subsequently return to their feeding areas in the spring when water temperatures rise. Thus, the turtles recaptured during more than one year of the study evidently returned to specific locations following seasonal migrations that sometimes span hundreds or even thousands of kilometers (Keinath 1993; Morreale and Standora 1995).

The navigational mechanisms underlying this ability are unknown. However, the directional headings and homing tracks obtained from telemetered turtles imply that displaced loggerheads were able to rapidly assess their position and then move toward the capture area. Turtles were apparently able to determine their position even after being transported along convoluted routes under conditions in which they could not view the sky or their surroundings. Thus, it is doubtful that the turtles determined the direction to travel using inertial (Etienne et al. 1996), landmark (Papi 1992), or compass (Wiltschko and Wiltschko 1978; Wehner et al. 1996) cues that were detected during displacement. Instead, it appears likely that the turtles determined their position relative to the capture area by relying on information available at the release site, an ability that fulfills the definition of map-based navigation (Able 2000). Although precisely how the turtles determined position cannot be inferred from this study, potentially available sources of positional information include chemical cues (Grassman et al., 1984), familiar landmarks (Wallraff et al. 1994), and magnetic field information (Lohmann and Lohmann 1996; 1998; Lohmann et al. 2001).

The recapture data were used to ascertain whether there was a difference between the sizes of turtles that were recaptured and those that were not. Turtles of a wide range

of sizes co-exist in the same habitat in Core Sound and it is possible that turtles of different sizes might exhibit different degrees of site fidelity, as is the case in some fishes (Gerking 1953; Parker and Hasler 1959; Yoshiyama et al. 1992; Huntingford et al. 1998) and snakes (Fraker 1970). In this study, however, no relationship was found between the size of loggerhead turtles and their tendency to home, or their tendency to remain in the capture area.

The recapture percentages observed for both displaced and non-displaced turtles are similar to those obtained for non-displaced loggerheads in Florida inshore waters (22%; Mendonca and Ehrhart 1982). In addition, the recapture rates are comparable to those of other experimentally displaced aquatic or semi-aquatic vertebrates such as spotted turtles, *Clemmys guttata*, (28%; Ernst 1968), English sole, *Parophrys vetulus*, (15%; Day 1976), senorita fish, *Oxyjulis californica*, (13-26%; Hartney 1996), and brown trout, *Salmo trutta* (18-21%; Halvorsen and Stabell 1990). However, while all four of the telemetered turtles in this study returned to the vicinity of their capture location within 3-5 d after release, only one was subsequently recaptured. These results suggest that the recapture rates obtained by sampling with pound nets probably underestimated the homing activity that actually occurred, as many turtles that return to the area may not enter the nets a second time.

Several other factors might also have decreased the number of individuals recaptured, yielding a conservative estimate of homing tendency. Some animal populations are known to consist of individuals that exhibit either resident or transient

behavior (Eifler and Eifler 1998). Thus, some of the turtles captured only once might have been transients or recent recruits that were not in an established home area, but instead were passing through the study location on their way to other destinations. Seasonal migrations might also temporarily increase the number of transient turtles. For example, during 1999 and 2000, there was a tendency for more turtles to be recaptured after having been displaced south versus north (Fig. 3). This tendency may reflect the recapture of turtles migrating through the inshore waters of North Carolina on their way to feeding areas further north such as Pamlico Sound, Chesapeake Bay, or Long Island Sound (Lutcavage and Musick 1985; Morreale 1992; Epperly et al. 1995a).

Because loggerheads feed opportunistically on many types of invertebrates, including patchily-distributed mollusks and mobile, widely-dispersed prey such as crustaceans and horseshoe crabs (Lutcavage and Musick 1985; Burke et al. 1993; Plotkin et al. 1993; Youngkin 2001), there is no obvious reason for a loggerhead to restrict its foraging activity to a small, localized area. Aerial survey data obtained during summer months (Epperly et al. 1995b) indicate that juvenile loggerheads are found throughout Core Sound, including areas near both the Shell Island Point and Cedar Island Point release sites (F. Gaskill, personal communication; NOAA Beaufort Laboratory, unpublished data). The presence of loggerheads in these areas suggests that suitable benthic foraging habitat exists near both locations where displaced turtles were released. Why then did many turtles return to their specific capture locations? While this study did not address the specific reasons for the turtles' return, it is possible that loggerhead distribution within Core Sound has been modified to some extent by the presence of

pound nets, which enable the turtles to obtain prey such as fish that they cannot otherwise capture. Thus, one possibility is that turtles are strongly motivated to return to the pound nets even after displacements because these areas represent locations that are unusually rich in resources (Stanley 1998).

The finding that juvenile loggerheads often exhibit homing behavior has implications for dredging operations in which turtles are displaced short to moderate distances from dredging equipment in an attempt to reduce turtle mortality (Dickerson et al. 1995). Little information is available to indicate whether turtles exhibit site fidelity to areas that are routinely dredged. However, some juvenile loggerheads captured in or near the regularly dredged shipping channel at Cape Canaveral, FL, U.S.A., have been recaptured in the area both within a given year and in different years (Henwood, 1987). In the present study, turtles displaced 20 km often returned to their capture locations within 3 to 5 d, and sometimes in as little as 24 h. Thus, if turtles captured at dredge sites display the same homing behavior as those in our study, then displacing them short distances is unlikely to be an effective means of reducing the likelihood that the turtles will interact with dredging equipment.

The present study provides evidence that juvenile loggerheads occupying inshore waters exhibit site fidelity to preferred areas and often home to those locations after displacement. In addition, the results demonstrate that some turtles returned repeatedly to specific sites during subsequent years after having migrated away from the area. However, further research is needed to determine the mechanisms underlying such

homing behavior, as well as the manner in which loggerheads use available foraging habitat.



## **CHAPTER 3**

### **HOMING BEHAVIOR AND MIGRATORY ORIENTATION IN JUVENILE LOGGERHEAD (*CARETTA CARETTA*) AND GREEN (*CHELONIA MYDAS*) SEA TURTLES**

#### **Introduction**

Many marine animals, including cetaceans (Würsig, 1989), pinnipeds (Condit and LeBouef, 1984; McConnell et al., 2002), tuna (Nemerson et al., 2000; Rooker et al., 2001), and marine turtles (Limpus, 1992; Meylan, 1995), migrate extensively throughout their lives. Quite often, these migrations take place across vast expanses of ocean that are seemingly devoid of guidance cues. Although the mechanisms used by hatchling sea turtles to orient and navigate have been extensively investigated (reviewed by Lohmann and Lohmann, 1998; Lohmann and Lohmann, in press), little is known about the cues used by older turtles, as well as other marine migrants. This is in part because studying orientation behavior in large, underwater animals that are powerful swimmers and range over large distances has proven difficult.

Juvenile sea turtles make attractive candidates for the study of orientation and navigation in marine migrants because they are small enough for laboratory studies. After a period of maturation spent in the open ocean, juvenile loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles from the east coast of the U.S.A. return to inshore waters and take up residence in feeding grounds (reviewed by Musick and Limpus, 1997). Juveniles of both species inhabit limited home ranges (Mendonca and

Ehrhart, 1982; Mendonca, 1983; Byles, 1988) and often exhibit homing behavior, returning rapidly to specific sites after being displaced (Ireland, 1980; Musick and Limpus, 1997; Avens et al., in press). Many turtles also undertake long-distance migrations between summer foraging grounds and overwintering areas (Morreale et al., 1992; Shoop and Kenney, 1992; Epperly et al., 1995a,b). Juveniles that spend their summers in the inshore waters of North Carolina, Virginia, and New York (Fig. 3.1) migrate south-southeast either to warmer, coastal waters or to the Gulf Stream during winter months (Shoop and Kenney, 1992; Keinath, 1993; Morreale and Standora, 1995; NOAA Beaufort Laboratory, unpub. data).

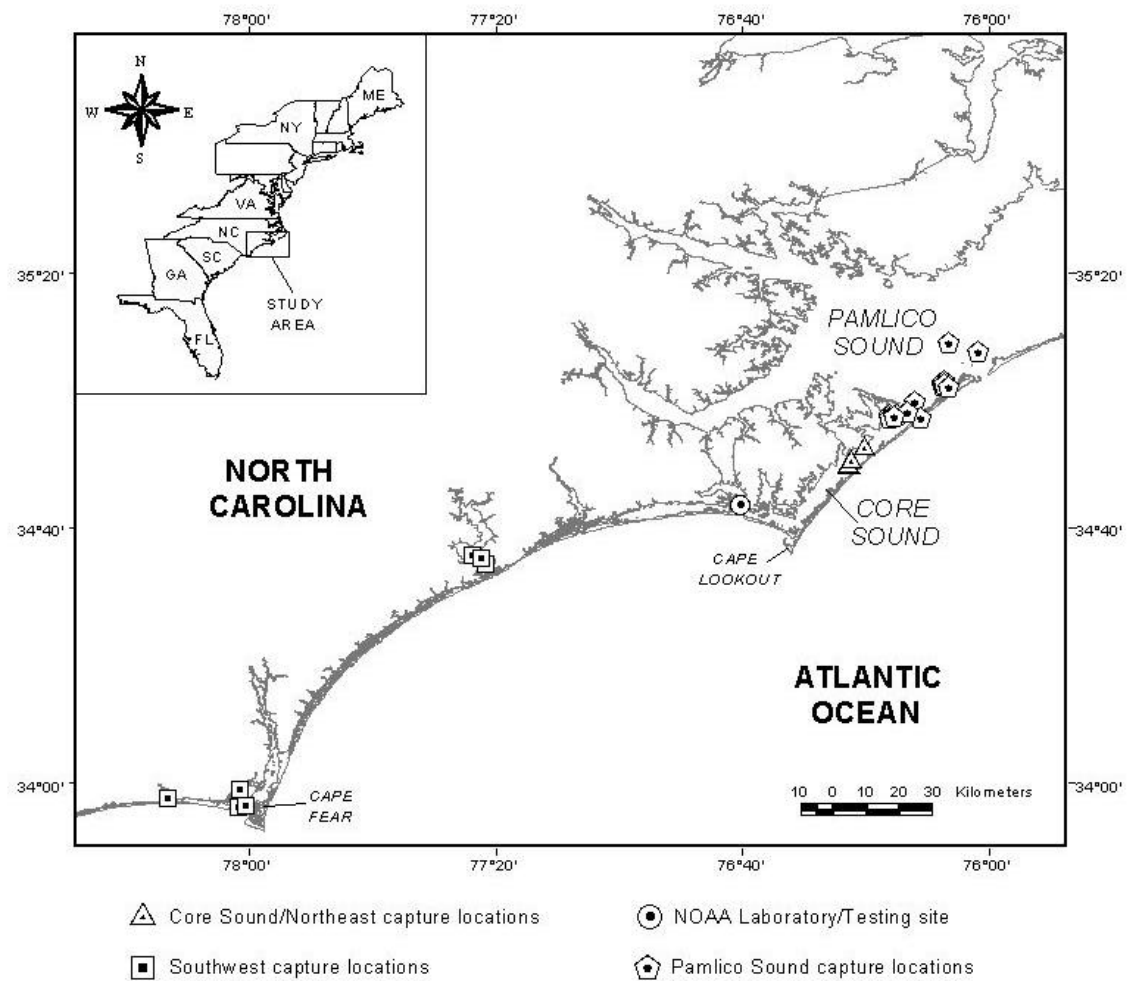
This study was conducted to investigate the orientation behavior and navigational abilities of juvenile sea turtles in a controlled environment. Juvenile loggerhead and green turtles were found to display homing and migratory behavior in a controlled setting. In addition, loggerheads appear to be able to determine the homeward direction on the basis of cues available at the test site, a result suggesting that they are capable of true navigation (Griffin, 1952; Phillips, 1996).

## **Materials and methods**

### *Experimental animals*

Juvenile loggerhead and green turtles were captured in the inshore waters of North Carolina, U.S.A. The majority of animals used in this study were caught in Core Sound and southern Pamlico Sound (Fig. 3.1) with pound nets. Although turtles were caught in Core Sound during the summer and the fall, they were only obtained from Pamlico Sound

Figure 3.1. Map of the coastal areas of North Carolina from which turtles were obtained for this study, showing capture locations in Core and Pamlico Sounds, as well as other inshore waters. The location of the testing site at the NOAA Laboratory is also shown.



during the fall because pound nets are generally only fished there during that time of year. For logistical reasons, fewer turtles were obtained from areas outside of Core and Pamlico Sounds (Fig. 3.1). All animals obtained from these other areas were loggerheads that were incidentally captured in gill nets, skimmer trawls, or in the cooling water intake canal at the Carolina Power & Light Nuclear Power plant in Brunswick Co., North Carolina. Juvenile loggerheads measuring 42.3-70.4 cm standard straight-line carapace length (SCL) and juvenile green turtles 21.2-44.0 cm SCL were retained for experiments. Each turtle was tagged to ensure that no turtle would be tested more than once.

All turtles were first transported by boat to shore and then by vehicle to the testing site. Turtles caught during fishing operations were prevented from viewing their surroundings and the sky and were transported to shore along a circuitous route. Loggerheads captured at the nuclear power plant intake canal were transported uncovered, first by boat and then in a truck, to a temporary holding facility, where they were held for less than 6 h.

After being transported to shore, all turtles were displaced to the National Oceanic and Atmospheric Administration (NOAA) Laboratory in Beaufort, North Carolina, where the study was conducted (Fig. 3.1). During displacement, turtles were placed into a covered truck, which prevented them from being able to view their surroundings and the sky, and transported along winding roads. The testing site was approximately 30 km from capture locations in Core Sound, 45-74 km from capture sites in Pamlico Sound, and 65-167 km from capture areas outside of Core and Pamlico Sounds.

At the laboratory, each turtle was placed into an outdoor, circular, holding tank measuring 2 m in diameter. Sea water was continuously circulated through the tanks and water depth was maintained at 0.75 m. Turtles were allowed to acclimate to captive conditions for approximately 24 h before being used in experiments. Each turtle underwent two trials, one each at the same time of day on two consecutive days (see Chapter 4). However, only data obtained from the first trial for each turtle were analyzed for the purposes of this study.

#### *Orientation arena and data acquisition*

Juvenile loggerheads were tested in an experimental arena (Fig. 3.2) consisting of a circular, fiberglass tank that was 6.1 m in diameter and 1.8 m high (Red Ewald, Karnes City, TX, USA). The arena, which was filled with sea water to a depth of 0.75 m, was located outdoors and was uncovered, allowing the turtles to see the sky. However, the walls of the tank blocked the turtles' view of the natural horizon and surroundings, with the exception of one tree branch that was visible to the north/northeast and the top of a building that was visible to the south/southwest.

During testing each loggerhead was outfitted with a nylon-lycra harness that encircled the carapace. The turtle was then tethered to a freely rotating arm mounted at the center of the arena (Fig. 3.2). As each turtle swam at the end of the tether, the arm followed, thus tracking the direction in which the turtle was swimming. A digital encoder coupled to the arm was wired to a nearby computer so that headings could be recorded to the nearest 1.4°.

Immediately before and after each trial, the tracking system was checked to ensure that the data acquisition system was functional and that the system registered a reading of 0° when the arm was pointing toward magnetic north. In addition, the water was stirred prior to each trial to ensure that no chemical gradients existed in the tank.

### *Testing procedure*

All experiments were conducted between May and November, months during which turtles are generally present in the inshore waters of North Carolina (Epperly et al., 1995a,b). Trials were conducted during daylight hours, between 12:30 and 17:00, under diverse weather conditions.

At the beginning of a trial, a turtle was tethered to the freely-rotating arm. To eliminate the possibility that the orientation of a turtle at the start of the trial might bias the direction a turtle swam, green turtles were released facing in random directions near the center of the arena. The much larger size of the loggerheads made it logistically impossible to release them from anywhere but a 1 m high platform located just outside the northern edge of the arena. We therefore attempted to eliminate directional bias for loggerheads by alternately placing them into the tank facing east or west.

After a turtle was tethered, it was allowed a 5 min acclimation period before the trial was initiated. Each trial was 10 min in duration, during which the computer recorded a directional heading every 30 s. A mean heading representing the average direction that the turtle swam during its 10 min trial and an *r*-value for that mean heading were then

calculated by the computer using standard procedures for circular statistics (Batschelet, 1981).

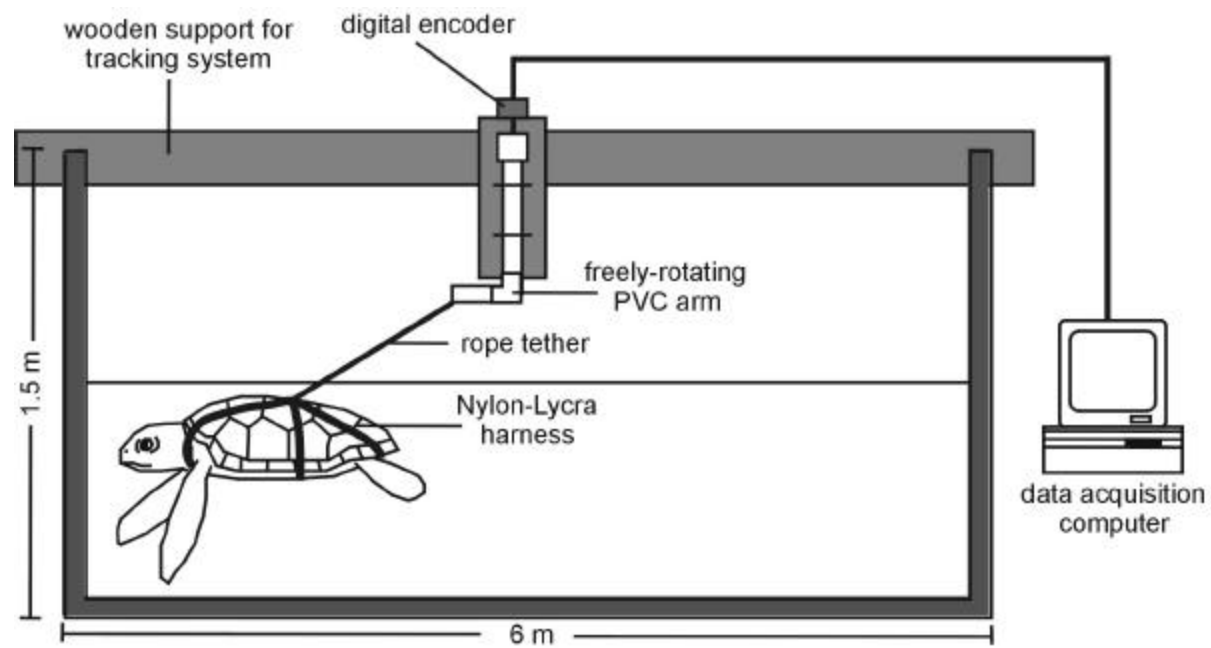
Trials were observed from a raised platform located approximately 5 m from the perimeter of the tank. Previous tests demonstrated that the presence of observers does not influence the orientation of turtles, provided that such observers do not approach the perimeter of the arena or cast shadows across the turtle's eyes (unpublished data). These observations are consistent with similar findings involving hatchling turtles (Salmon and Lohmann, 1989) and are also not surprising because sea turtles are myopic when their eyes are in air (Ehrenfeld and Koch, 1967). Animals were monitored to ensure that they swam consistently at the end of the tether. Turtles were eliminated from the study if their behavior met the following criteria three times at the moment at which the computer recorded a heading during a trial: 1) the direction the freely-rotating arm was facing did not represent the turtle's direction of orientation or 2) a turtle did not swim, i.e. sat motionless at the bottom of the tank. Those turtles that did not swim consistently were replaced with other, more active individuals.

#### *Data analysis*

In North Carolina, sea turtles occupy inshore waters approximately from April through September and begin to emigrate when water temperatures drop during October and November (Epperly et al., 1995a). Therefore, data obtained between May and September ('summer') were analyzed to determine whether turtles exhibited orientation



Fig. 3.2. Schematic of the experimental arena and the data acquisition system used to monitor the orientation of juvenile loggerhead sea turtles (turtle not drawn to scale). Each turtle was outfitted with a nylon-lycra harness and tethered to a freely-rotating arm in the arena. The data acquisition computer was located in a shed approximately 5 m to the south of the arena. See text for details of testing procedure.



consistent with homing behavior. Data collected during October and November ('fall') were analyzed to determine whether turtles exhibited seasonally appropriate migratory orientation. Because turtles were obtained from Pamlico Sound solely during the fall, no data for turtles caught in this area were used in the homing analysis.

The distributions of headings for turtles tested during the summer were analyzed using the V-test in conjunction with calculation of the 95% confidence interval. This was done to determine whether turtles in each group were significantly oriented in a direction that was consistent with the direction of their capture location (Batschelet, 1981). The homeward direction for loggerhead and green turtles captured in Core Sound, to the northeast of the testing site, was  $74^{\circ}$ . Because loggerheads obtained to the southwest of the testing site were caught at several different locations (Fig. 3.1), an average homeward bearing ( $255^{\circ}$ ) was calculated for these turtles and this bearing was used for analysis. Watson's  $U^2$  test was applied to ascertain whether the headings of loggerheads obtained to the northeast and to the southwest were significantly different from one another (Batschelet, 1981).

Given that no specific expected direction was known for turtles tested during October and November, data obtained from turtles tested during the fall were analyzed using the Rayleigh test to determine whether the turtles were significantly oriented (Batschelet, 1981). Watson's  $U^2$  test was used to ascertain whether the orientation of loggerhead and green turtles in the fall was significantly different from that observed during the summer (Batschelet, 1981).

## Results

### *Summer orientation*

During trials conducted between May and September ('summer'), juvenile loggerheads captured to the northeast of the testing site from 1998 through 2001 were significantly oriented in a direction that corresponded with the most direct path back to their capture area (Mean angle =  $83^{\circ}$ ,  $p < 0.0005$ , V-test, 95% confidence interval  $\pm 25^{\circ}$ )(Fig. 3.3A; see Fig. 3.4A-D for data from individual years). Similarly, juvenile green turtles obtained to the northeast during the same time of year were also significantly oriented toward their capture site (Mean angle =  $50^{\circ}$ ,  $p < 0.0025$ , V-test, 95% confidence interval  $\pm 37^{\circ}$ )(Fig. 3.5A).

Loggerheads captured to the southwest of the testing site during the summer were significantly oriented with a mean heading consistent with the direction of their respective capture locations (Mean angle =  $271^{\circ}$ ,  $p < 0.05$ , V-test, 95% confidence interval  $\pm 76^{\circ}$ )(Fig. 3.3B). This heading was significantly different from that obtained for juvenile loggerheads caught to the northeast that were tested during the same time of year ( $p < 0.001$ ; Watson's  $U^2$  Test).

The behavior of loggerheads while swimming in the arena differed from that of the green turtles. While only 16% of loggerheads tested in the arena were rejected under the criteria set forth in the methods, 50% of green turtles were eliminated from the study because of their failure to swim consistently at the end of the tether.

### *Fall orientation*

Juvenile loggerheads obtained from northeast of the testing site during October and November ('fall') oriented with a mean heading of  $190^{\circ}$  ( $p < 0.005$ ; Rayleigh test, 95% confidence interval  $\pm 33^{\circ}$ ) (Fig. 3.3C). This direction of orientation was significantly different from that observed for loggerheads obtained to the northeast and tested during the summer ( $p < 0.001$ ; Watson's  $U^2$  Test). Similarly, green turtles tested during the fall were significantly oriented with a mean heading of  $199^{\circ}$  ( $p < 0.02$ ; Rayleigh test, 95% confidence interval  $\pm 39^{\circ}$ ) (Fig. 3.5B), which was significantly different from the mean heading found for green turtles tested during the summer ( $p < 0.02$ ; Watson's  $U^2$  Test).

## **Discussion**

### *Homing behavior*

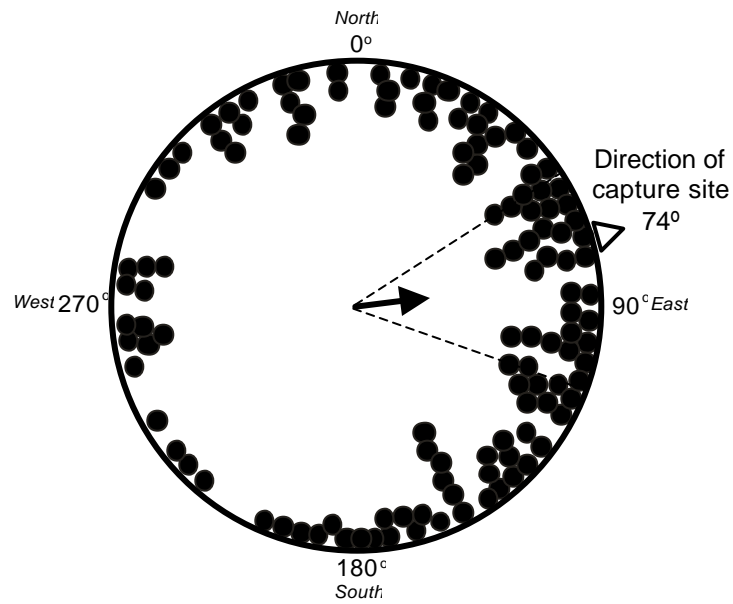
Juvenile loggerhead turtles obtained from areas both to the northeast and to the southwest of the testing site oriented toward their respective capture locations during summer months (Fig. 3.3A,B; Fig. 3.4A-D). Thus, these results imply that they were capable of determining the direction of their capture site, or their 'homeward' direction, after being passively displaced 30-167 km to an unfamiliar location. To accomplish this, it was presumably necessary to first determine geographic position relative to home.

In principle, displaced turtles might use several different navigational mechanisms to determine their position. One such mechanism is route-based navigation, during which animals monitor the outward path from a location using inertial (Etienne, 1996), landmark (W. Wiltschko and Wiltschko, 1978), or compass cues (R. Wiltschko and

Fig. 3.3. Summer and fall orientation of juvenile loggerhead turtles. Each dot within a circular diagram represents the mean angle of orientation for a single turtle over its 10-minute trial and the triangles on the outside of the circles correspond to the home direction for each group of turtles tested. The dotted lines represent the 95% confidence interval for the mean heading. (A) Summer orientation of loggerheads tested May-September, 1998-2001. Turtles with a home bearing of  $74^{\circ}$  were significantly oriented with a mean angle of  $83^{\circ}$  ( $n=122$ ,  $r=0.29$ ,  $p<0.0005$  V-test, 95% confidence interval  $\pm 25^{\circ}$ ). (B) Summer orientation of loggerheads tested May-September, 1999-2001. Turtles with an average home bearing of  $255^{\circ}$  were significantly oriented with a mean angle of  $271^{\circ}$  ( $n=11$ ,  $r=0.43$ ,  $p<0.05$  V-test, 95% confidence interval  $\pm 76^{\circ}$ ). (C) Fall orientation of loggerheads tested October-November, 1998-2000. Turtles oriented with a mean heading of  $190^{\circ}$  ( $n=15$ ,  $r=0.61$ ,  $p<0.005$  Rayleigh test, 95% confidence interval  $\pm 33^{\circ}$ ), a direction of orientation consistent with that observed in wild turtles at that time of year.

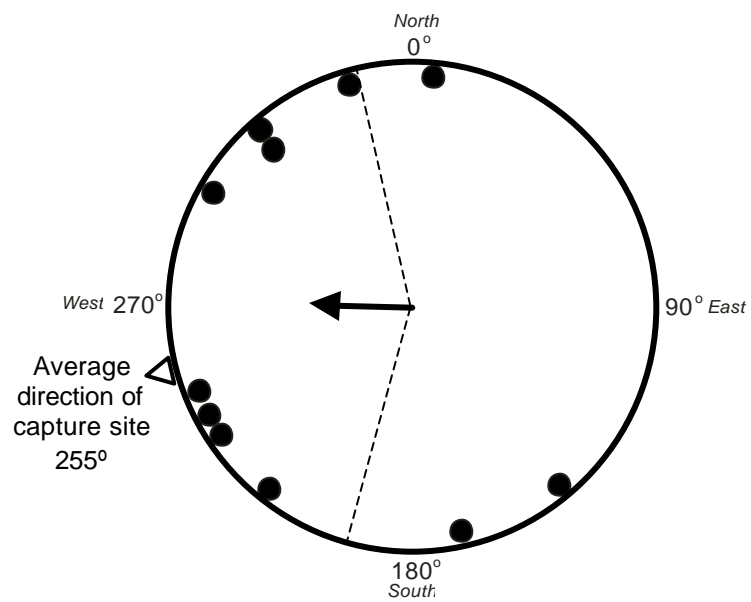
A)

Summer orientation of loggerhead turtles  
captured northeast of testing site



B)

Summer orientation of loggerhead turtles  
captured southwest of testing site



C)

Fall orientation of loggerhead turtles  
captured northeast of testing site

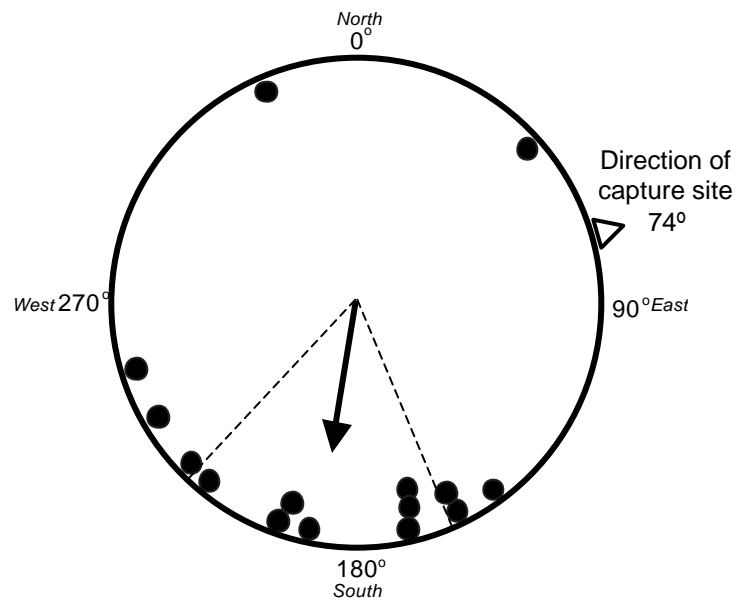
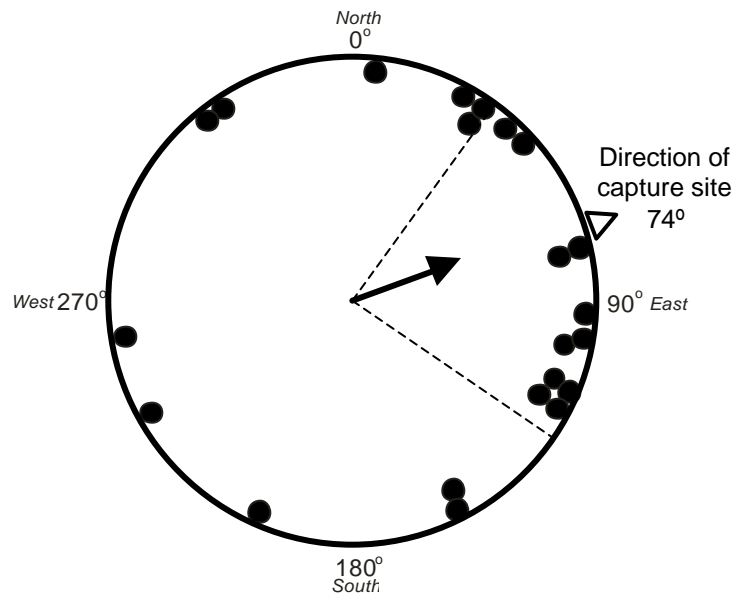




Fig. 3.4. Summer orientation of juvenile loggerhead turtles each year from 1998 to 2001. Each dot within a circular diagram represents the mean angle of orientation for a single turtle over its 10-minute trial and the triangles on the outside of the circles correspond to the home direction for each group of turtles tested. The dotted lines represent the 95% confidence interval for the mean heading. Direction of capture site for each year was 74°. (A) Orientation of loggerheads tested May-September, 1998. Turtles were significantly oriented with a mean angle of 80° (n=22,  $r=0.42$ ,  $p<0.005$  V-test, 95% confidence interval  $\pm 44^\circ$ ). (B) Orientation of loggerheads tested May-September, 1999. Turtles were not significantly oriented with a mean angle of 45° (n=29,  $r=0.09$ ). (C) Orientation of loggerheads tested May-September, 2000. Turtles were significantly oriented with a mean angle of 102° (n=38,  $r=0.33$ ,  $p<0.005$  V-test, 95% confidence interval  $\pm 42^\circ$ ). (D) Orientation of loggerheads tested May-September, 2001. Turtles were significantly oriented with a mean angle of 73° (n=33,  $r=0.38$ ,  $p<0.001$  V-test, 95% confidence interval  $\pm 39^\circ$ ).

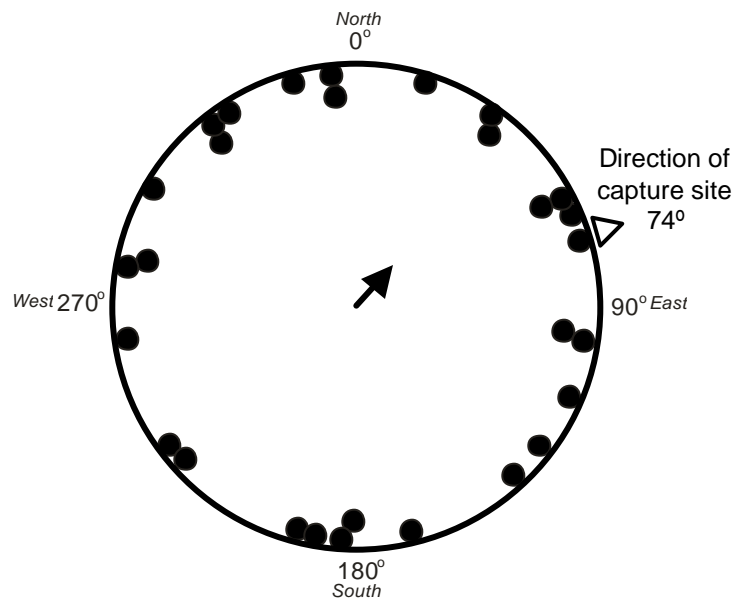
A)

Summer orientation of loggerhead turtles  
captured northeast of testing site during 1998



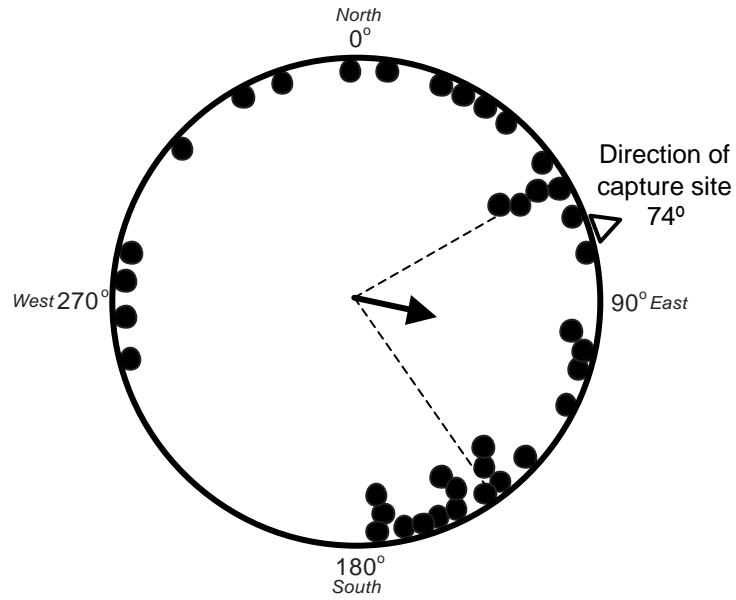
B)

Summer orientation of loggerhead turtles  
captured northeast of testing site during 1999



C)

Summer orientation of loggerhead turtles  
captured northeast of testing site during 2000



D)

Summer orientation of loggerhead turtles  
captured northeast of testing site during 2001

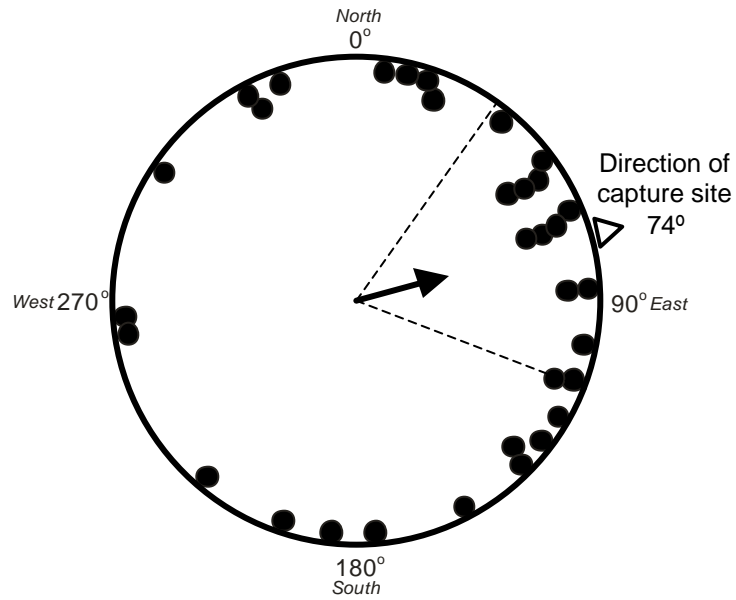
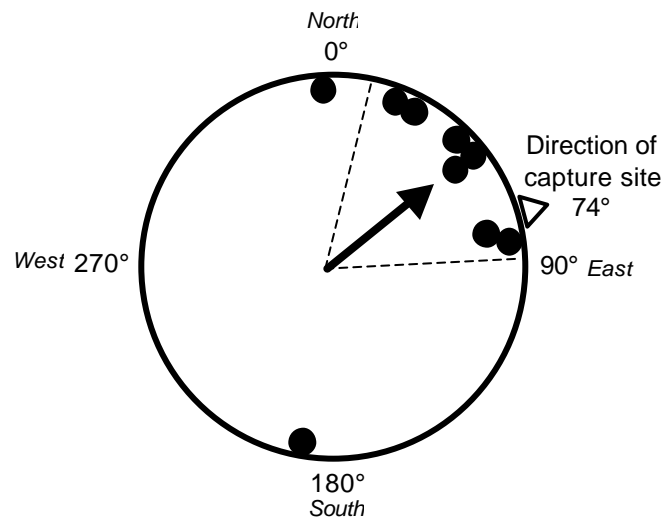


Fig. 3.5. Summer and fall orientation of juvenile green turtles. Each dot within a circular diagram represents the mean angle of orientation for a single turtle over its 10-minute trial and the triangles on the outside of the circles correspond to the home direction for each group of turtles tested. The dotted lines represent the 95% confidence interval for the mean heading. (A) Summer orientation of green turtles tested May-September, 1998-1999. Turtles with a home bearing of  $74^\circ$  were significantly oriented with a mean angle of  $50^\circ$  ( $n=9$ ,  $r=0.71$ ,  $p<0.0025$  V-test, 95% confidence interval  $\pm 37^\circ$ ). (B) Fall orientation of green turtles tested October-November, 1998 and 2001. Turtles oriented with a mean heading of  $199^\circ$  ( $n=7$ ,  $r=0.76$ ,  $p<.02$  Rayleigh test, 95% confidence interval  $\pm 39^\circ$ ), a direction of orientation consistent with that observed in wild turtles at that time of year.

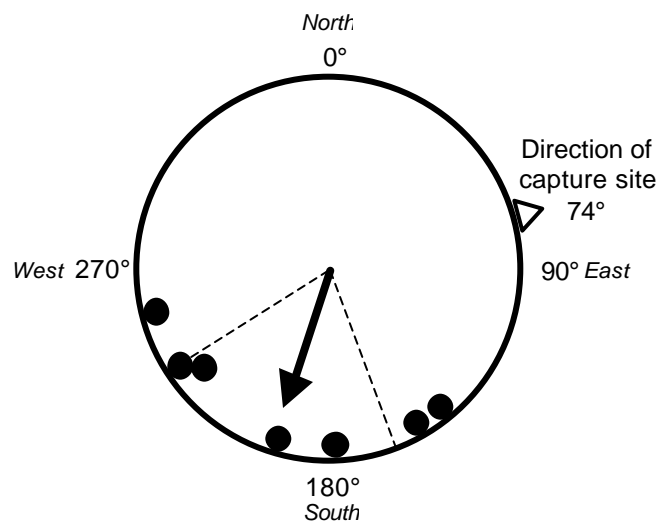
A)

Summer orientation of green turtles  
captured northeast of testing site



B)

Fall orientation of green turtles  
captured northeast of testing site



Wiltschko, 1978; Wehner et al., 1996) and integrate that information to determine the return course (W. Wiltschko and Wiltschko, 1978; Able, 2000). It seems improbable, however, that the turtles used this mechanism. Inertial cues appear to be insufficient to accurately monitor passive displacements even over short distances (Bovet, 1992; Etienne, 1996), much less the long displacements experienced by turtles in this study. Furthermore, visual cues were blocked during transport, eliminating the possibility that landmarks or a celestial compass sense could be used to monitor the displacement. Hatchling loggerheads possess a magnetic compass sense (Lohmann, 1991) that could, in principle, be used as a reference during route-based navigation. However, it is unlikely that a magnetic compass would have allowed the turtles to determine the direction and distance of the extremely circuitous displacement routes.

The turtles' ability to orient toward their capture areas from an unfamiliar location in the absence of route-based information and sensory contact with the goal is consistent with map-based navigation, as defined by Griffin (1952) and Phillips (1996). In the context of homing, animals capable of map-based navigation can ascertain their geographic position relative to home using only local cues available at the release or testing site (Griffin, 1952; Phillips, 1996). Local cues might include components of a mosaic map, such as landmarks or odors (W. Wiltschko & Wiltschko, 1978; Papi, 1991; Able, 2000), or magnetic features (Phillips, 1996). However, because the turtles were not able to view the surroundings outside the tank, they could not have used a mosaic map consisting of visual landmarks to determine their position. Although the possibility that turtles might use a mosaic map of odors cannot be excluded completely, it is unlikely that

all turtles tested had previously visited the study area to learn its characteristic odor, as well as the spatial relationship between the testing site and home.

Experiments involving a number of different animals, including sea turtles, have provided evidence to support the use of the earth's magnetic field in position-finding (Munro et al., 1997; Fischer et al., 2001; Franson et al., 2001; Phillips et al., 2002; Boles and Lohmann, 2003; reviewed by Lohmann and Lohmann, in press). Loggerhead hatchlings can detect both the inclination angle (Lohmann and Lohmann, 1994) and intensity (Lohmann and Lohmann, 1996) of the earth's magnetic field and alter their orientation in response to changes in those parameters. Moreover, hatchling loggerheads exposed to combinations of inclination and intensity that are found around the North Atlantic Gyre exhibit directional orientation that would keep them within the confines of the gyre (Lohmann et al., 2001). These components therefore appear to provide the hatchlings with at least a rudimentary sense of geographic position. Thus, if juvenile sea turtles retain the ability to sense the same magnetic field parameters as hatchlings, then the turtles tested during this study might have been able to use magnetic information to determine their geographic location.

The homing orientation exhibited by the turtles during this study is consistent with results of other displacement studies in which turtles were moved away from their capture sites and released. Ireland (1980) found that, of 10 juvenile green turtles displaced 1.5-4 km from their capture sites and followed using sonic telemetry, 70% returned to the capture area within 2 d of release. Similarly, out of 27 adult female

loggerheads that were captured on nesting beaches before they had the opportunity to lay their eggs, displaced approximately 60 km, and followed using radio telemetry after release, 85% exhibited homing behavior within 2 to 6 d (Murphy and Hopkins-Murphy, 1990). Furthermore, during the mark-recapture study described in Chapter 2, 20% of juvenile loggerheads displaced 15 to 20 km from their capture sites in inshore waters were recaptured, often within a few days of being released (see also Avens et al., in press). Taken together, the turtles' rapid returns to their respective capture areas strongly suggest that displaced turtles can, in fact, determine their geographic position relative to the capture site.

In contrast to the results of these studies, the authors of one study conducted using nesting turtles from Ascension Island (Luschi et al., 2001) concluded that female green turtles do not possess a positional sense that would enable them to return to specific sites. During that study, the turtles were displaced 60-450 km from their nesting beaches, outfitted with satellite transmitters that would allow the researchers to remotely track the turtles' movements, and released. Many of these turtles ultimately began the return migration to their feeding grounds instead of moving back toward Ascension Island. The paths of those turtles that did return to the nesting beach were somewhat convoluted, leading the researchers to speculate that the turtles found the beach either by random wandering or by smelling odors carried from the island on the prevailing winds.

It is possible that the navigational capabilities of various turtle populations may differ and that the green turtles nesting on Ascension Island are not capable of position-



finding. However, it is also possible that the discrepancy between the results of this study and those mentioned above were the result of procedural differences. During the Ascension Island study, satellite transmitters were attached to the head instead of to the carapace, as in most other telemetry studies involving sea turtles (Keinath et al., 1993; Plotkin et al., 1995; Morreale, 1999; Hays et al., 2001). Evidence suggests that, in vertebrates, magnetoreceptors are probably located in the head (Walker et al., 1997; Deutschlander et al., 1999; Phillips et al. 2001). The strong magnetic pulses produced when the transmitters emitted radio signals could therefore have disrupted magnetic information that the Ascension Island turtles might normally have used to navigate. In addition, while Murphy and Hopkins-Murphy (1990) displaced nesting loggerheads *before* they were able to deposit their eggs, Luschi et al. (2001) displaced their nesting greens *after* they had nested. It is likely that the turtles captured prior to nesting had a far greater motivation to return to the nesting beach than those turtles that had already deposited a clutch of eggs and were entering a two-week interesting period during which activity levels might typically be reduced (Houghton et al., 2002). Thus, additional studies are needed to determine whether the apparent failure of the Ascension Island green turtles to return to their nesting beaches is attributable to an inability to navigate or to other, unrelated factors.

### *Migratory orientation*

The results demonstrate that juvenile loggerhead and green turtles will display seasonal migratory orientation in a controlled setting. While turtles tested during summer months exhibited orientation that coincided with their homeward directions (3.3A,B;

3.4A-D; 3.5A), turtles tested in the fall oriented southward (Fig. 3.3C; 3.5B). This orientation behavior during the migratory season closely parallels the restlessness exhibited by captive, migratory birds (W. Wiltschko and Wiltschko, 1991). Researchers have been able to exploit this behavior to investigate the many factors underlying migration in these birds, including the cues used to orient and navigate (Munro et al., 1997; Wiltschko et al., 1998), the genetic basis of migratory orientation (Helbig, 1996; Pulido et al., 2001), and the circannual rhythms involved in migration (Gwinner, 1996). The orientation behavior exhibited by juvenile sea turtles in the present study has the potential to allow researchers to study the migratory behavior of sea turtles in a similar manner.

## **CHAPTER 4**

### **USE OF MULTIPLE ORIENTATION CUES BY JUVENILE LOGGERHEAD SEA TURTLES (*CARETTA CARETTA*)**

#### **Introduction**

Sea turtles migrate extensively throughout their lives (Carr, 1987; Bowen et al., 1995; Meylan, 1995; Bolten et al., 1998). Although the orientation cues used by hatchling sea turtles have been investigated in considerable detail (reviewed by Lohmann et al., 1997; Lohmann and Lohmann, in press), little is known about the guidance mechanisms used by older turtles. In many animals, the strategies and mechanisms used in orientation and navigation change as individuals mature, gain experience, and take up residence in new habitats (Wiltschko, 1983; Baker, 1984; Rodda and Phillips, 1992; Able and Able, 1996; Wiltschko and Wiltschko, 1998). Thus, directional and positional cues used by juvenile and adult turtles might differ significantly from those used by hatchlings.

Numerous cues are potentially available to juvenile and adult sea turtles during their extensive migrations and movements. Hatchlings are able to set and maintain headings based on wave direction (Lohmann et al., 1990; Lohmann and Lohmann, 1992), the Earth's magnetic field (Lohmann, 1991), or interactions between the two (Goff et al., 1998), and similar abilities are likely to persist in older turtles. Other cues that might provide directional information under at least some conditions include chemical gradients

(Koch et al., 1969), celestial features such as the sun or polarized light (DeRosa and Taylor, 1980; Hawryshyn et al., 1990), and familiar landmarks (Luschi et al., 1996). At present, however, little direct evidence exists to indicate which, if any, of these cues are actually used by juvenile and adult turtles.

To investigate the directional cues used by older turtles, juvenile loggerheads were studied to determine whether they were able to maintain consistent directional headings in the absence of wave cues, familiar landmarks, and chemical gradients. The turtles were also tested under conditions in which magnetic cues were disrupted, visual cues were disrupted, or both were disrupted together. The results demonstrate that juvenile loggerheads use multiple cues to orient and can maintain headings using either magnetic or visual information, depending on which is available.

## **Materials and methods**

### *Animals*

Juvenile loggerhead sea turtles (*Caretta caretta*) were captured with pound nets in Core Sound, North Carolina, U.S.A. Loggerheads ranging from 42.3 to 67.4 cm standard straight-line carapace length were retained for experiments. They were then transported to the National Oceanic and Atmospheric Administration (NOAA) Laboratory in Beaufort, North Carolina, approximately 30 km southwest of the capture area. There, each turtle was placed into an outdoor, circular tank measuring 2 m in diameter. Sea water was continuously circulated through the tanks and water depth was maintained at 0.75 m. Turtles were allowed to acclimate to captive conditions for about 24 h before

being used in experiments. Each turtle was used for only one set of experimental trials (see General experimental protocol) before being released.

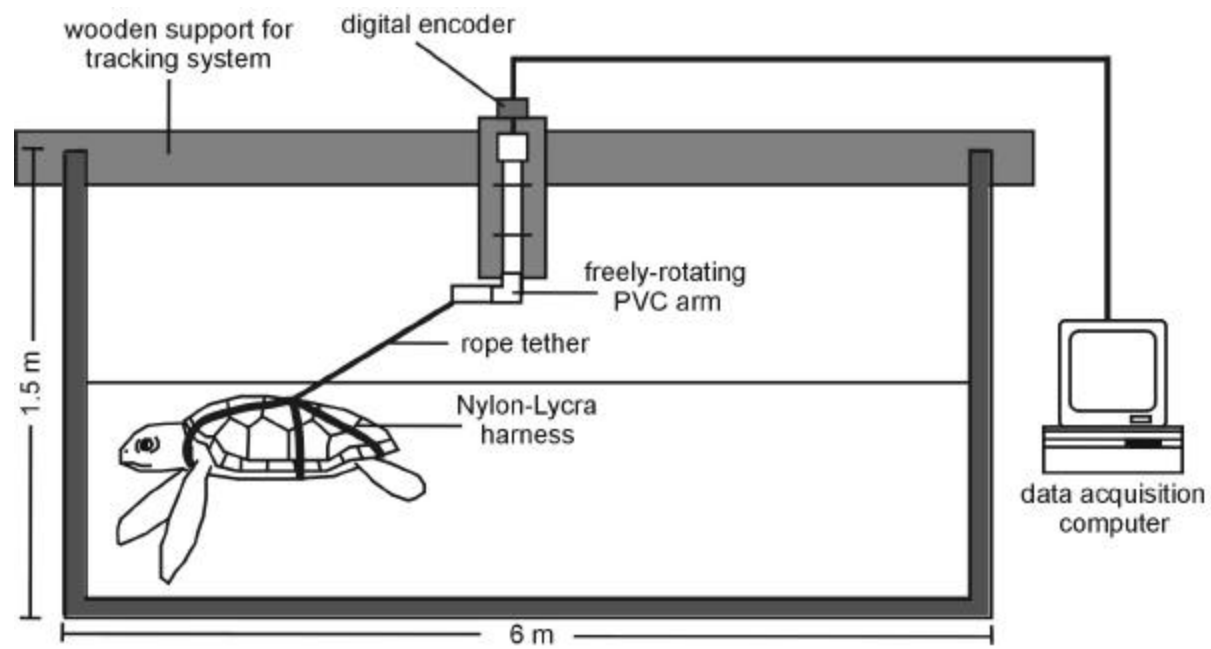
#### *Orientation arena and data acquisition*

Juvenile loggerheads were tested in an experimental arena (Fig. 4.1) consisting of a circular, fiberglass tank that was 6.1 m in diameter and 1.8 m high (Red Ewald, Karnes City, TX, USA). The arena, which was filled with sea water to a depth of 0.75 m, was located outdoors and was uncovered, allowing the turtles to see the sky. However, the walls of the tank blocked the turtles' view of the natural horizon and surroundings, with the exception of one tree branch that was visible to the north/northeast and the top of a building that was visible to the south/southwest.

During testing each loggerhead was outfitted with a nylon-lycra harness that encircled the carapace. The turtle was then tethered to a freely rotating arm mounted at the center of the arena (Fig. 4.1). As each turtle swam at the end of the tether, the arm tracked the direction in which the turtle was swimming. A digital encoder coupled to the arm was wired to a nearby computer so that headings could be recorded to the nearest 1.4°.

Immediately before and after each trial, the tracking system was checked to ensure that the data acquisition system was functional and that the system registered a reading of 0° when the arm was pointing toward magnetic north. In addition, the water was stirred prior to each trial to ensure that no chemical gradients existed in the tank.

Figure 4.1. Schematic of the experimental arena and the data acquisition system used to monitor the orientation of juvenile loggerhead sea turtles (not to scale). Each turtle was outfitted with a Nylon-Lycra harness and tethered to a freely-rotating arm in the arena. The data acquisition computer was located inside a shed located approximately 5 m to the south of the arena. See text for details of testing procedure.



### *General experimental protocol*

All experiments were conducted between May and November, months when turtles inhabit the sounds of North Carolina (Epperly et al., 1995a). Trials were carried out during daylight hours between 12:30 and 17:00 h.

At the beginning of a trial, a turtle was tethered to the freely-rotating arm. Turtles were alternately placed into the tank facing east and west to eliminate any bias in orientation that might arise by releasing all turtles facing the same direction. After a turtle was tethered, it was allowed a 5-min acclimation period before the trial was initiated. During the next 10 min, the data acquisition computer recorded the turtle's directional heading every 30 s. A mean angle representing the average direction that the turtle swam during its 10-min trial was then calculated by the computer.

Trials were observed from a raised platform located approximately 5 m from the perimeter of the tank. Previous tests demonstrated that the presence of observers does not influence the orientation of turtles, provided that such observers do not approach the perimeter of the arena or cast shadows across the turtle's eyes (unpublished data). These observations are consistent with similar findings involving hatchling turtles (Salmon and Lohmann, 1989) and are also not surprising because sea turtles are myopic when their eyes are in air (Ehrenfeld and Koch, 1967). Turtles were monitored to ensure that they swam consistently at the end of the tether. Those that did not were replaced with other, more active individuals.



Preliminary experiments demonstrated that when tested during trials conducted on several different days, the headings of individual turtles were usually consistent from day to day. Thus, a turtle that swam east during its first trial was likely to swim approximately east when tested again the next day, whereas a turtle that swam north the first time usually also swam approximately north when tested again. This observation provided the basis of the procedures developed for use in subsequent experiments.

During experiments, each turtle was tested in the arena at the same time of day on two consecutive days. On the first day, the turtle swam in the unaltered local magnetic field with a full view of the sky; these results were used to determine the individual's preferred direction of orientation under the test conditions. On the second day, turtles were randomly assigned to several treatment groups and tested again, either under the same conditions or under new conditions in which one or more orientation cues were manipulated (see below). This approach enabled us to determine which treatments affected the turtles' orientation behavior, and thus to infer which cues are used by the turtles to maintain consistent headings.

### *Magnetic impairment experiments*

An experiment was first conducted to determine if disrupting the magnetic field around the turtles affected orientation if visual cues remained available. We focused the magnetic disruption on the anterior part of the body because evidence suggests that, in vertebrates, magnetoreceptors are probably located in the head (Walker et al., 1997; Deutschlander et al., 1999; Phillips et al. 2001). Ceramic magnets with fields measuring

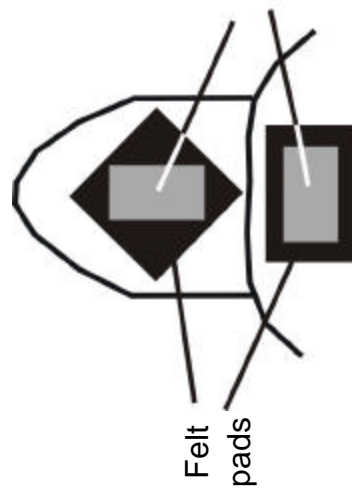
4000  $\mu\text{T}$  at 1 cm from the magnet's surface (8 cm L x 6 cm W x 1 cm H; Magnet Sales & Manufacturing, Inc., CA) were attached to both the dorsal surface of the head and the anterior margin of the carapace (Fig. 4.2). Pads of felt material were affixed to the head and carapace using cyanoacrylate adhesive and magnets were then attached to the felt pads using plastic electrician's ties. This arrangement allowed the magnets to shift position slightly as the turtles swam, producing a strong, constantly changing magnetic field.

All trials were conducted under clear or partly cloudy skies when the sun was visible. Turtles were divided into four treatment groups for Day 2 trials. One group, which served as a control, was tested in the same way as on Day 1 ( $n = 13$ ). Turtles in two additional groups were tested with magnets attached to them. In the south-up group ( $n = 16$ ), both magnets were arranged so that the field lines leaving the magnet were directed downward and the south pole of the magnet was up. In the north-up group ( $n = 13$ ), both magnets were arranged in the opposite way so that the north pole of each magnet was up. Turtles in the fourth group were equipped with two brass bars that were the same mass as the magnets but did not disrupt the magnetic field ( $n = 15$ ). In all cases, magnets or brass bars were attached to the turtles immediately prior to testing.

### *Visual impairment experiments*

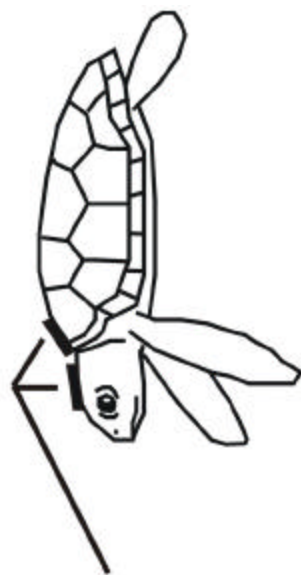
A second experiment was carried out to determine whether eliminating visual cues disrupted orientation if magnetic cues remained undisturbed. To block visual cues,

Figure 4.2. Diagram of magnet and brass bar attachment to loggerhead turtles. Felt pads were attached to the dorsal surface of the head and the anterior margin of the carapace using cyanoacrylate adhesive and magnets or brass bars sewn into felt pouches were attached to the felt pads using electrician's ties.



Magnets  
or Brass  
bars

Felt  
pads



(Top view)

(Side view)

turtles were outfitted with goggles (Fig. 4.3), which were attached using cyanoacrylate adhesive and were easily removed after completion of a trial.

Turtles were divided into three treatment groups on Day 2. One group was tested in the same way as during Day 1 (no treatment) ( $n = 8$ ). A second group was outfitted with goggles containing frosted, plastic lenses that blocked the turtles' view of their surroundings and the sky and also depolarized the light passing through the lenses (Fig. 4.3) ( $n = 9$ ). Although some light still penetrated the frosted lenses, a human observer looking through the lenses on sunny days was not able to localize the position of the sun. To control for possible effects of goggle attachment, a third group was outfitted with goggle frames containing no lenses ( $n = 9$ ). Goggles or goggle frames were attached to the turtles immediately prior to testing.

#### *Combined magnetic and visual impairment experiments*

A final experiment was conducted to determine if simultaneously disrupting magnetic and visual cues affected the orientation of the turtles. Turtles were divided into three treatment groups on Day 2. Turtles in all three groups were equipped with goggles containing frosted lenses. In addition, turtles in the first group were outfitted with south-up magnets ( $n = 8$ ), turtles in the second group carried north-up magnets ( $n = 10$ ), and turtles in the third group were outfitted with non-magnetic brass bars ( $n = 10$ ).

Fig. 4.3. Photograph of a juvenile loggerhead outfitted with goggles containing frosted lenses. The goggle frames were attached to the turtle using cyanoacrylate adhesive and fit closely to the contours of the turtle's head. Turtles were therefore unable view the sky through gaps between the frames and the head.



### *Data analysis*

A mean heading and *r*-value were calculated for each trial using standard procedures for circular statistics (Batschelet, 1981). Because different turtles swam toward different directions during Day 1 trials, each turtle's mean angle during its first trial was normalized to 0°. The angular difference between each turtle's heading on Day 2 versus that on Day 1 was then plotted relative to 0° (Lohmann et al. 1995). Thus, for example, a turtle that had a mean angle of 90° during its first trial and a mean angle of 110° during its second would be scored as an angle of 20°. This procedure enabled us to compare the responses of turtles to the different treatments by determining whether animals in each group maintained their original Day 1 courses (toward 0°) or changed direction.

For each treatment, distributions were analyzed by using the V-test with an expected direction of 0° (the direction that turtles would be expected to swim if they did not change headings between Day 1 and Day 2). For distributions in which the V-test indicated statistically significant orientation, a 95% confidence interval was calculated for the mean heading to determine if the direction of orientation was consistent with the expected direction (Zar, 1996). The Mardia-Watson-Wheeler test was used to determine if differences existed among the results obtained from the various treatment groups in each experiment (Batschelet, 1981).



## Results

### *Behavior of tethered turtles*

Most turtles swam steadily while tethered, sometimes switching among powerstroking (which involves moving both front flippers synchronously) in mid-water, alternating flipper strokes while moving along the bottom of the tank, and dogpaddling when surfacing to breathe (Wyneken, 1997). Although the turtles spent the majority of their trials actively swimming, they occasionally sat motionless at the end of the tether for a brief time before resuming activity.

Whereas some turtles adopted consistent headings almost immediately after being introduced to the tank, others circled for several minutes before doing so. Once a course had been established, however, the orientation of the turtle was typically highly consistent for the duration of the trial (Fig. 4.4).

### *Magnetic impairment experiments*

Turtles in all groups maintained approximately the same headings on Day 2 that they had maintained on Day 1, regardless of whether they carried magnets, brass bars, or neither (Fig. 4.5A-D). No significant differences existed among the headings of the four treatment groups ( $W = 2.18$ ,  $p > 0.81$ ; Mardia-Watson-Wheeler Test).

### *Visual impairment experiments*

None of the three groups (control turtles, turtles wearing goggles without lenses, or turtles wearing frosted lenses) deviated significantly from their Day 1 headings when

Figure 4.4. Representative orientation of three different juvenile loggerhead turtles tethered in the experimental arena. A different symbol (black squares, black triangles, or open diamonds) denotes each turtle. Time is indicated along the horizontal axis and the angle of orientation is indicated along the vertical axis. Each dotted line represents the mean heading of the turtle over its 10 min trial. Once a turtle established a course, it typically maintained relatively consistent headings for the duration of the trial.

Representative orientation of juvenile loggerheads tethered in the experimental arena

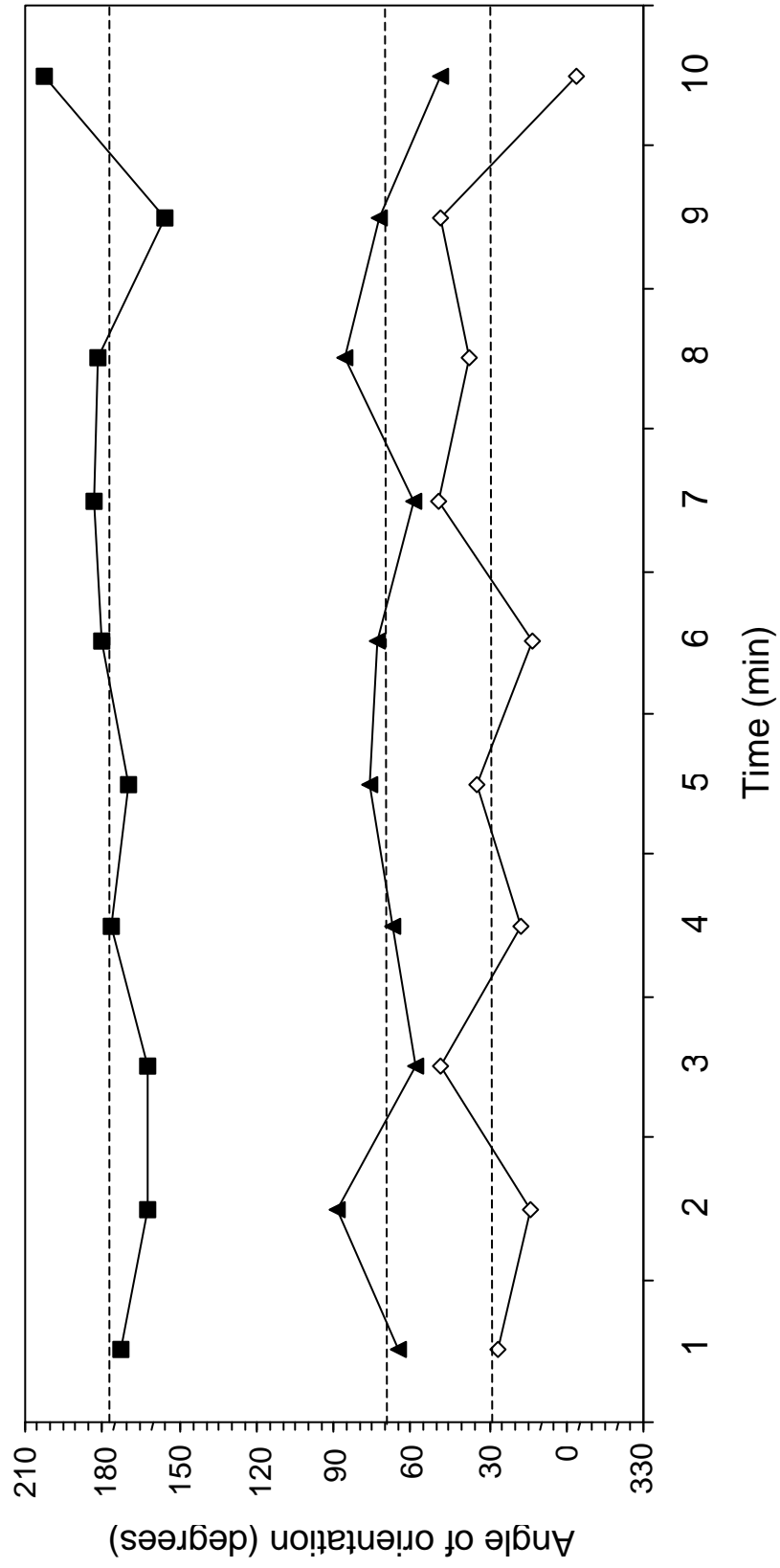


Figure 4.5. Results of magnetic impairment experiment. Each dot represents the angular difference between an individual turtle's mean heading on Day 2 versus Day 1. All four groups of turtles oriented in the expected direction of 0°. (A) No treatment: mean angle=0°,  $r=0.50$ ,  $p<0.005$  V-test, 95% confidence interval  $\pm 49^\circ$ ; (B) Brass bars: mean angle=26°,  $r=0.35$ ,  $p<0.05$  V-test, 95% confidence interval  $\pm 90^\circ$ ; (C) North-up magnets: mean angle=12°,  $r=0.46$ ,  $p<0.025$  V-test, 95% confidence interval  $\pm 56^\circ$ ; (D) South-up magnets: mean angle=357°,  $r=0.34$ ,  $p<0.05$  V-test, 95% confidence interval  $\pm 90^\circ$ . See text for statistical comparison of distributions.

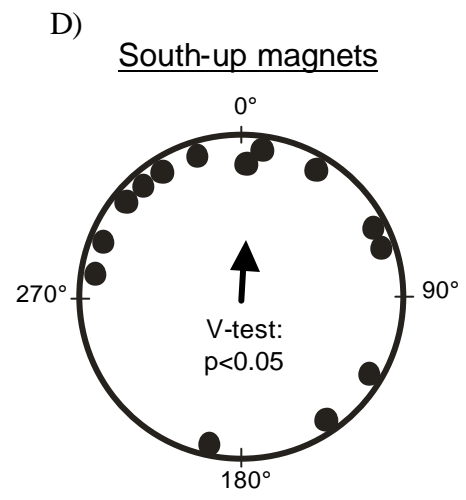
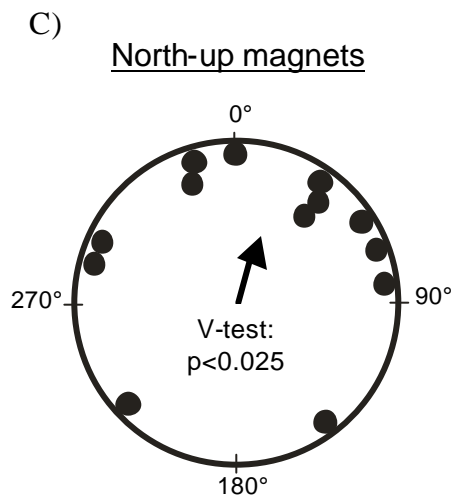
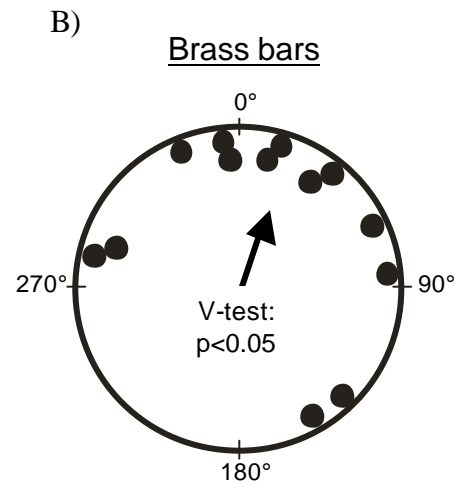
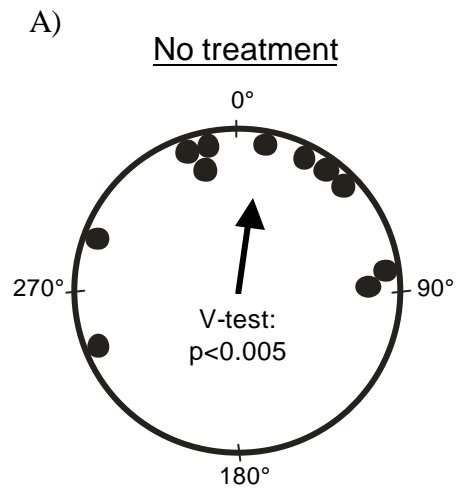
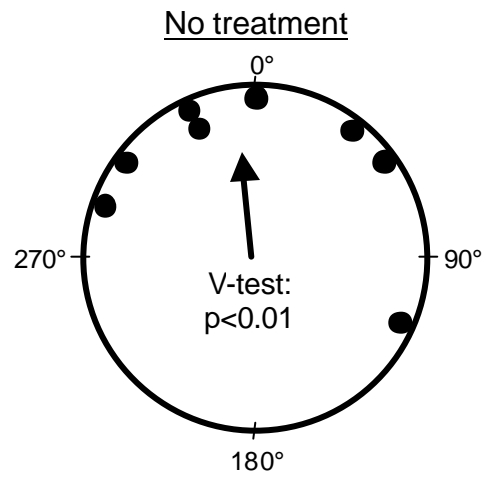


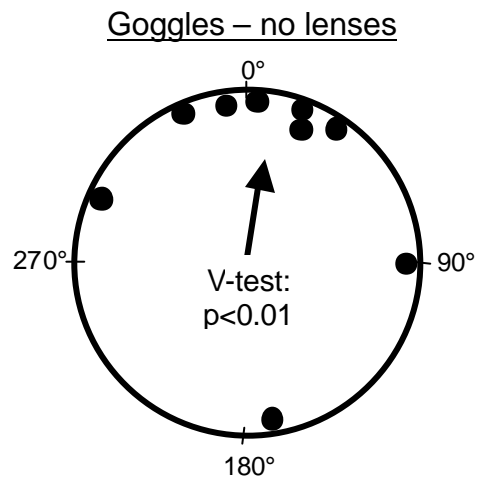
Figure 4.6. Results of visual impairment experiment. Each dot represents the angular difference between an individual turtle's mean heading on Day 2 versus Day 1.

Loggerheads in all three treatment groups were able to maintain a direction of orientation from Day 1 to Day 2. (A) No treatment: mean angle= $356^{\circ}$ ,  $r=0.61$ ,  $p<0.01$  V-test, 95% confidence interval  $\pm 51^{\circ}$ ; (B) Goggles with no lenses: mean angle= $9^{\circ}$ ,  $r=0.58$ ,  $p<0.01$  V-test, 95% confidence interval  $\pm 51^{\circ}$ ; (C) Goggles containing frosted lenses: mean angle= $335^{\circ}$ ,  $r=0.60$ ,  $p<0.01$  V-test, 95% confidence interval  $\pm 48^{\circ}$ . The expected direction in all cases was  $0^{\circ}$ . See text for statistical comparison of distributions.

A)



B)



C)

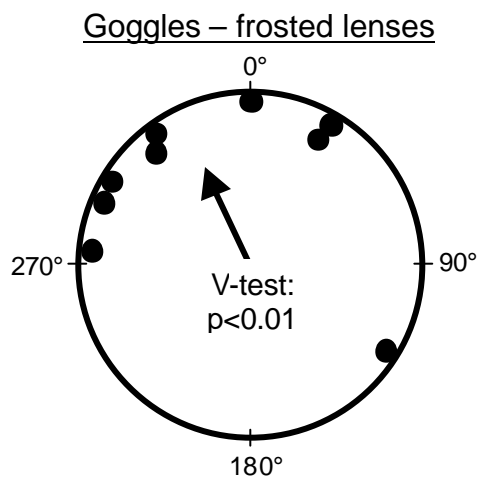
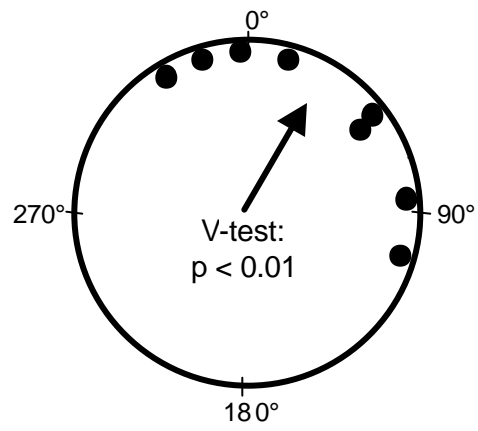


Figure 4.7. Results of combined magnetic and visual impairment experiment. Each dot represents the angular difference between an individual turtle's mean heading on Day 2 versus Day 1. Turtles wearing frosted goggles and outfitted with brass bars were able to maintain a direction of orientation from Day 1 to Day 2 in the expected direction of  $0^\circ$ , while those bearing frosted goggles and magnets did not do so. (A) Brass bars + Frosted goggles: mean angle= $31^\circ$ ,  $r=0.69$ ,  $p<0.01$  V-test, 95% confidence interval  $\pm 41^\circ$ ; (B) South-up magnets + Frosted goggles: mean angle= $196^\circ$ ,  $r=0.65$ , n.s. V-test; (C) North-up magnets + Frosted goggles: mean angle= $110^\circ$ ,  $r=0.37$ , n.s. V-test. See text for statistical comparison of distributions.



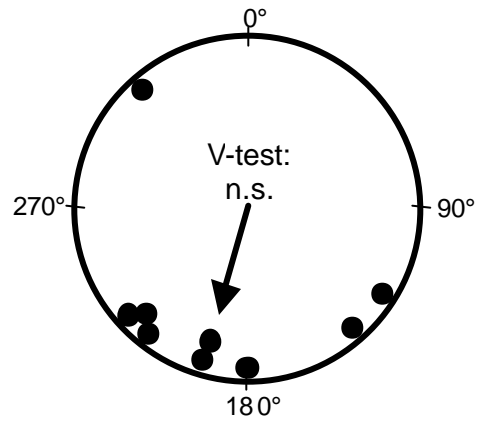
A)

Brass bars + Frosted goggles



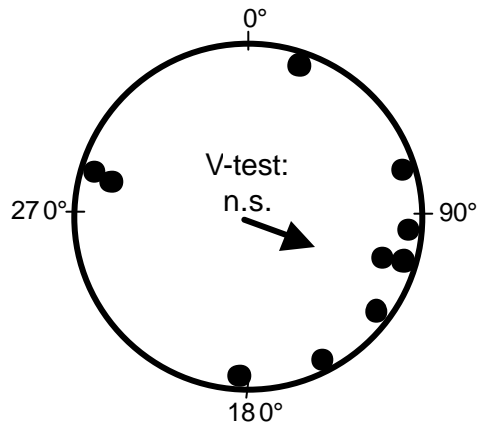
B)

S-up magnets + frosted goggles



C)

N-up magnets + frosted goggles



tested on Day 2 (Fig. 4.6A-C). No significant differences existed among the three distributions ( $W = 2.18$ ,  $p = 0.56$ ; Mardia-Watson-Wheeler Test). Turtles wearing goggles with frosted lenses appeared to swim normally and their behavior did not differ in any obvious way from that of the other groups.

#### *Combined magnetic and visual impairment experiments*

Turtles outfitted with frosted goggles and non-magnetic brass bars oriented toward approximately the same direction on both Day 1 and Day 2 (Fig. 4.7A). In contrast, those loggerheads outfitted with frosted goggles and magnets in either the North-up or South-up position did not do so (Fig. 4.7B,C). The Mardia-Watson-Wheeler test indicated that significant differences existed among the three groups ( $W = 11.89$ ,  $p = 0.02$ ).

### **Discussion**

Juvenile loggerheads tethered in an experimental arena established and maintained directional headings in the absence of wave cues, familiar landmarks, and chemical gradients (Figs. 4.4, 4.5A, 4.6A, 4.7A). Although the results do not eliminate the possibility that turtles use some or all of these cues in other settings, they imply that turtles under the test conditions relied on other cues to maintain orientation.

Turtles with unimpaired vision that swam in a distorted magnetic field did not orient differently from those in control groups (Fig. 4.5A-D). Similarly, turtles wearing goggles that deprived them of visual cues did not orient differently from control turtles if the magnetic environment around them was undisturbed (Fig. 4.6A-C). However,

significant differences in orientation were found among the groups of turtles that either only experienced magnetic impairment or were simultaneously deprived of both magnetic and visual (Fig. 4.7A-C). Taken together, these results imply that juvenile loggerheads possess at least two different means of maintaining a heading. When only magnetic cues were disrupted, the turtles could apparently compensate by using visual information; when only visual cues were disrupted, the turtles could rely on magnetic information. When both cues were simultaneously disrupted, however, then the turtles' orientation was altered.

#### *Magnetic cues*

The results imply that juvenile loggerheads used a magnetic compass to orient when visual cues were not available. A magnetic compass has been previously demonstrated to exist in both loggerhead (Lohmann, 1991; Light et al., 1993) and leatherback (*Dermochelys coriacea*) turtle hatchlings (Lohmann and Lohmann, 1993). In these young turtles, the magnetic compass presumably helps hatchlings maintain an offshore heading during their migration from their natal beaches to the open ocean (reviewed by Lohmann and Lohmann, in press). The results of the present study provide strong evidence that juvenile loggerheads are able to maintain consistent headings by using the Earth's field in a manner similar to that observed in hatchlings.

#### *Visual cues*

Although depriving turtles of both visual and magnetic information evidently affected their orientation (Fig. 4.7B,C), the orientation of turtles with access to visual

information alone did not differ from that of control turtles (Fig. 4.5C,D). These data imply that swimming turtles can exploit visual cues to maintain headings. Although the results do not enable us to determine the precise type of visual information that was used, two types of celestial cues appear to be good candidates. One possibility is that juvenile loggerheads possess a time-compensated sun compass, as is present in numerous animals including pigeons (Schmidt-Koenig, 1960; Schmidt-Koenig et al., 1991), freshwater and terrestrial turtles (DeRosa and Taylor, 1980), fish (Hasler et al., 1958; Winn et al., 1964; Levin et al., 1992), and various invertebrates (von Frisch, 1967; Scapini et al., 1999; Mouritsen and Frost, 2002). Alternatively or additionally, turtles might exploit patterns of skylight polarization. This cue is used by desert ants during path integration (Wehner et al., 1996), by birds during migratory movements (Able and Able, 1993, 1996), and by several fish species (Waterman and Forward, 1970; Hawryshyn et al., 1990).

#### *Use of multiple orientation cues*

The results indicate that juvenile loggerhead sea turtles are able to use at least two different directional cues to maintain headings. These results closely parallel findings reported in several other animals (Quinn and Brannon, 1982; Sinsch, 1990; reviewed by R. Wiltschko and Wiltschko, 1995; Wiltschko et al., 1998). For example, young sockeye salmon (*Oncorhynchus nerka*) are able to orient using both celestial cues and a magnetic compass (Quinn, 1980). Similarly, homing pigeons use a time-compensated sun compass when the sun is visible (Schmidt-Koenig, 1960; reviewed by Schmidt-Koenig, 1991), but rely on a magnetic compass when skies are overcast (Keeton, 1971; Ioalè, 2000).

In juvenile loggerheads, the relative importance of the different cues is not yet known. In principle, turtles might behave similarly to pigeons, using solar cues when they are available but relying on magnetic cues when the sky is overcast or when water visibility is poor. Because migrating loggerheads are active at night as well as during the day (Nichols et al., 2000), turtles might also rely on magnetic cues at night when the sun is not visible.

Apart from studies involving hatchlings (reviewed by Lohmann et al., 1997; Lohmann and Lohmann, 1998), most prior investigations of sea turtle orientation and navigation have been conducted in the ocean, where numerous cues are often available and the ability to control sources of directional and positional information is at best limited. The techniques developed for this study demonstrate for the first time that the orientation mechanisms of juvenile turtles can be studied in a more controlled environment in which cues can be manipulated with relative ease. Thus, the findings set the stage for additional investigations of the mechanisms underlying orientation and navigation in juvenile and adult sea turtles.

## **CHAPTER 5**

### **SUMMARY**

Sea turtles migrate extensively throughout their lives. This extremely migratory lifestyle is similar to that of other large, marine animals such as cetaceans and pinnipeds in that migrations take place across vast expanses of seemingly featureless ocean. Although the guidance mechanisms used by hatchling sea turtles during the offshore migration away from their natal beaches have been extensively investigated, the cues used by juvenile and adult turtles remain unknown. The present study sought to use juvenile sea turtles as a novel system for the study of sea turtle navigation. Specifically, the purpose of this study was to 1) determine whether juvenile loggerhead sea turtles inhabiting the inshore waters of North Carolina exhibit site fidelity and homing behavior in the wild, 2) ascertain whether juvenile loggerhead and green sea turtles exhibit homing orientation and seasonally appropriate migratory orientation in a controlled setting and to determine if homing was accomplished using true navigation, and 3) investigate the sensory cues used by juvenile loggerheads to orient.

To investigate site fidelity and homing behavior in juvenile loggerheads occupying inshore waters, a mark-recapture study spanning four years was conducted in Core Sound, North Carolina. Each year of the study, approximately half of the turtles captured were tagged and released near the capture site, while the other half was displaced 15-20

km and released. Radio telemetry was also used to more closely follow the movements of a small number of turtles following displacement.

Analysis of the recapture data showed that turtles were often recaptured both during the same year that they were tagged, as well as during subsequent years after having completed seasonal migrations. Furthermore, the proportions of turtles recaptured after being tagged and released near the capture location and after being displaced were not significantly different from one another. These data imply that juvenile loggerheads will home following displacement, because if turtles dispersed randomly or remained near their release sites, fewer displaced turtles would be predicted to be recaptured. Four displaced turtles were successfully followed using radio telemetry and these individuals rapidly returned to their capture areas. However, three of the four turtles were not recaptured, suggesting that the mark-recapture data underestimate the true extent of both site fidelity and homing behavior in these animals. Taken together, these results indicate that juvenile loggerheads exhibit fidelity to preferred foraging areas during summer months and possess the navigational abilities to home to these areas following long-distance migrations and forced displacements.

Experiments were also conducted to determine if juvenile sea turtles would exhibit homing and seasonal migratory orientation in a controlled setting, as well as to ascertain whether the turtles were capable of true navigation. Juvenile loggerheads were displaced from capture locations to the northeast and southwest of a testing site during the summer and allowed to swim in an experimental arena to determine whether individuals from

both sites exhibited orientation consistent with the most direct path back to their respective capture areas. In addition, both loggerhead and green turtles captured to the northeast were tested to determine whether they would exhibit homeward orientation during the summer and southward, migratory orientation during the fall.

Juvenile loggerheads captured to both northeast and southwest of the testing location exhibited orientation consistent with the most direct path back to their respective capture sites. The turtles appeared to be able to determine their geographic position relative to their capture sites based solely on local cues, suggesting that juvenile loggerheads are capable of true navigation. Both loggerhead and green turtles obtained to the northeast exhibited homeward orientation during the summer, when turtles would be expected to occupy foraging areas in inshore waters. In addition, the turtles exhibited southward orientation during the fall, a direction that corresponds to the migratory orientation observed in wild turtles at that time of year.

Finally, experiments were conducted to investigate the orientation cues used by juvenile loggerheads. Turtles were tested in the experimental arena to determine whether they could maintain headings in preferred directions in the absence of familiar landmarks and chemical gradients. In addition, turtles experience 1) magnetic impairment, 2) visual impairment, or 3) both magnetic and visual impairment to determine which of these cues were necessary for the turtles to maintain their headings.



Juvenile loggerheads tested in the experimental arena were able to set and maintain consistent directional headings in the absence of familiar landmarks when no chemical gradients were present. Turtles were also able to maintain a direction of orientation when either the magnetic field surrounding the anterior portion of the body was disrupted or when visual cues were blocked, but were no longer able to maintain their headings when both cues were simultaneously altered. These results demonstrate that juvenile loggerheads are capable of using both magnetic and visual cues to orient, depending on which is available.

The results of the study of site fidelity and homing behavior in the wild have implications for the conservation of threatened loggerhead sea turtles. Dredges are regularly used to deepen shipping channels and the use of hopper dredges has been implicated in the mortality of large numbers of turtles. In an attempt to minimize turtle take, efforts have been made to remove turtles from a given channel and to release them some distance away from the proposed dredging site. In this study, however, loggerhead turtles displaced moderate distances were able to return to their capture locations very rapidly. Therefore, this strategy should not be used during seasons when turtles are foraging in the areas to be dredged without additional research to determine whether longer displacement distances might prove more effective.

The results of the investigation of homing behavior and seasonal migratory orientation in the experimental arena provide future researchers with a novel means of studying the orientation and navigation of sea turtles. As a result of using this method, it

was possible for the first time to determine some of the sensory cues that might be used to guide juvenile sea turtles during short-distance movements, as well as during longer migrations. Nonetheless, much research is still necessary before we fully understand the mechanisms used by sea turtles to orient and navigate throughout their lives.

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